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THE UNIVERSITY OF ALBERTA

Faunal Similarity and Infracommunity Structure in the
Helminths of Lesser Scaup

by



Albert O. Bush

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

ZOOLOGY

EDMONTON, ALBERTA

FALL, 1980

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Faunal Similarity and Infracommunity Structure in the Helminths of Lesser Scaup submitted by Albert O. Bush in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Abstract

The faunal similarities among the helminth infracommunities of 45 lesser scaup, Aythya affinis, from 13 lakes, representing 3 distinct biomes in Alberta, were compared using a variety of multivariate techniques.

Recurrent group analysis revealed a single group of 9 commonly co-occurring species. No subsidiary groups could be formed.

Cluster analysis revealed an overall high degree of similarity in the helminth faunas of lesser scaup, with little tendency for infracommunities from the same lake to be more similar to each other than to infracommunities from different lakes. Clusters were based primarily on differences in abundance of the common species.

Principal components and Varimax rotated factor analyses revealed two intermediate host suites of parasites, one using Hyalella azteca, the other using Gammarus lacustris. Very high frequency, abundance, and intercorrelation of abundances within suites, plus the fact that they use the preferred food of lesser scaup, suggested that these species are truly characteristic of that host. Furthermore, the evidence suggested that the similarity between infracommunities attributable to the intermediate host suites (plus other frequent species) was greater than the similarity attributable to biotic or abiotic characteristics of the lakes.

The structure of the infracommunities was investigated in terms of the linear distributional features of helminth species and niche overlaps between species. These data were then compared to predictions of random models.

The frequent species showed restricted distributions and predictability in their sequence of occurrence along the gut. A test of inter-niche distances (as measured by distances between median points) against a random model suggested more regularity in the distribution of species than predicted by chance. The large absorber guild preferred the mid- and posterior regions of the gut; the non-absorbers preferred the anterior. Both groups were significantly different from random distributions but collectively they suggested an even spread across the intestine.

The low overlaps among the frequent species suggested that they differed significantly in their niche exploitation patterns whereas the high overlaps among infrequent species suggested a high degree of similarity in their niche exploitation patterns. Most of the realized niche overlaps (average niche overlaps) among the frequent species were significantly smaller than their fundamental overlaps (summed niche overlaps). This significant reduction, from fundamental overlap to realized overlap, was interpreted as evidence for interaction between these species. Most of the realized niche overlaps among the infrequent species were not significantly different from fundamental overlaps. This was considered evidence for lack of interaction among these

species.

A summary of the evidence suggested two components in the infracommunities: the deterministic component composed of waterfowl generalists and lesser scaup specialists, and the stochastic component composed of specialists in other hosts.

Preface

A Chemist Looks At Parasitology

Parasitology! Parasitology!
One part of science to two of mythology,
Doodles of doodles that you will insist
Are micro-sized monsters that just can't exist,
Papers replete with long names in italics
Describing in jargon the fanciful antics
Of creatures who live on the fat of the land
In host after host without lifting a hand.
Parasitology! Queen of Biology!
One part of science to two of mythology.
Don't you owe nature a humble apology?

Written by Dr. A.E.R. Westman for
the retirement of Dr. A. M. Fallis
31 May, 1972, Toronto

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Karen Neilsen provided valuable laboratory assistance

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important, goes to my wife, Margaret. She did all of the things most graduate students wives do, from typing and editing to drawing figures (the difference between those drawn by her and those drawn by myself are, unfortunately, all too obvious). Most important, however, she provided an environment of love, understanding, and, during those crucial times when things seemed overwhelmingly bleak, encouragement.

TABLE OF CONTENTS

Chapter	Page
I. Introduction	1
II. The System	9
An Abundant and Motile Habitat	9
A Single Resource Axis	10
Populating the Host - Immigration and Death	12
The Intestinal Guild	14
III. Study Areas	16
IV. Methods and Materials	21
Helminthology	21
Estimates of Lake Biota	24
Analytical Methods	27
V. The Helminth Fauna	35
VI. Faunal Similarity	41
Recurrent Groups	41
Recurrent Groups of Helminths in Lesser Scaup	43
Persistence Stability of Recurrent Group Species	56
Discussion	62
Cluster Analysis	65
Clustering of Lakes by Helminth Faunas	69
Discussion	79
Principal-Components and Rotated Factor Analysis	81

Table of Contents (continued)

Chapter	Page
Principal-Component and Rotated Factor Analysis of Helminths in Lesser Scaup	82
Discussion	91
Faunal Similarity - Concluding Discussion	94
VII. Infracommunity Structure	98
Linear Distributions of Scaup Helminths	100
Discussion	108
Community Models	110
Intestinal Helminth Parasites and the Broken-Stick Model	112
Discussion	122
Patterns of Interaction	123
Discussion	132
Infracommunity Structure - Concluding Discussion	133
VIII. Unpublished Remarks	138
Literature Cited	146
Appendices	175

LIST OF TABLES

Table	Description	Page
1.	Selected abiotic features for each lake	20
2.	Semi-quantitative data on invertebrate and fish collections	25
3.	Numerical abundance of bird groups on each lake	28
4.	Subjective ranks of six most abundant bird species on each lake	30
5.	Frequency, abundance, and distribution of all helminth species found in 5 or more hosts	36
6.	Selected lake features used in rank correlation analysis	54
7.	Significant rank correlations between selected lake features and recurrent group species	57
8.	Rotated factor analysis of abundant helminths	87
9.	Rotated factor analysis of recurrent group species	92
10.	Significant correlations between abundance and respective anterior or posterior endpoints and ranges	103
11.	Comparison of selected niche distances between observed and predicted	118
12.	Characteristics of the deterministic and stochastic components in lesser scaup infracommunities	139

LIST OF FIGURES

Figure		Page
1.	Map of collection areas in Alberta	18
2.	Trellis diagram of species forming the recurrent group	46
3.	Trellis diagram of Kendall's Tau between abundance of 16 frequent species	49
4.	Diagram of abundance correlations	51
5.	Cluster dendrogram for entire dataset	72
6.	Cluster dendrogram for all species in 5 or more hosts	75
7.	Cluster dendrogram for recurrent group species	78
8.	Plot of first and second principal components for all species in 5 or more hosts	85
9.	Plot of first and second principal components for recurrent group species	90
10.	Comparison between linear distributions from Hair (1975) and the current study	106
11.	Plot of niche distances for the 8 species infracommunities based on De Vita's model	114
12.	Standard deviations of mean niche distances for all infracommunities	117
13.	Comparison of average versus summed niche overlaps using symmetrical measure	129
14.	Comparison of average versus summed niche overlaps using asymmetrical measure	131

I. Introduction

"But it is time for a speculative phase in the development of the ecology and evolution of parasites"

Peter W. Price, *Evolutionary Biology of Parasites*, 1980

Are there features of the environment that account for similarity of composition between communities? Are there features which provide for structure within communities? These questions seem to be the major stimuli that have generated research in community ecology for decades. They permeate both the early research, which focused primarily on describing the elements of the community, and current research which attempts to elucidate the underlying mechanisms that contribute to the similarity between, and structure within, communities.

These questions suggest two principle lines of research, the first of which concerns similarity of composition. As successive observations are made in different areas, the fidelity of certain species to particular habitats raises questions about the nature of the habitat, or of the species themselves, that accounts for, or allows, this fidelity. Repetitive observations on a single area often suggest some level of organization within a community and thus generate questions on how, or why, a community is assembled or structured. Plant ecologists

appear to have been the first to recognize repetitive associations and the different frequencies of species occurrences in similar associations (e.g., Gleason, 1920; Braun-Blanquet, 1932; Raunkiaer, 1934). These early observations led to widely divergent views of the nature of the community and the inherent similarity between some communities. Tansley (1935) viewed the community as an integrated fundamental unit, having discrete boundaries, and amenable to classification. Gleason (1926) on the other hand, was a leading proponent of the individualistic view in which the community, as a unit, is merely a convenient abstraction used by ecologists to classify what is simply a collection of populations with similar environmental requirements. This latter view led to the development of gradient analysis as a technique for studying populations on a continuum and led to attempts at correlating species distributions with environmental variables (e.g., Whittaker, 1967).

Zoologists seem to have avoided being drawn into the discontinuous versus continuous controversy yet are still very much concerned with similarity questions. This is perhaps most evident in the literature on marine invertebrate faunas where many studies have shown that certain species of plankton can be grouped by their apparent fidelity to particular water bodies (examples in Rottman, 1978). The term recurrent group has been coined for these associations of seemingly allied species and their

recognition has led to a new generation of analyses designed to compare similarities of faunas (Egger, 1957; Stephenson, 1972; Wishart, 1978). Although the controversies are not as pronounced, nor the techniques necessarily the same, zoologists are addressing essentially the same questions as the botanists: are there recurrent groups and, if so, are they correlated with particular environmental variables such that they characterize a specific habitat?

The second line of research concerns structure within the community and has been primarily the province of zoologists. Perhaps one of the greatest challenges in this area has been the Competitive Exclusion Principle attributed to Gause (1934). Stated simply: two species with identical requirements cannot coexist simultaneously in the same area. Observations on natural communities, however, often reveal closely related species living together in apparently the same habitat. Several mechanisms have been proposed to explain this coexistence and the inherent effect on community structure. Two of these competition (leading to niche differentiation) and predation (acting to prevent competitive exclusion), seem to generate the greatest controversy. Some authors (e.g., Pianka, 1978) suggest that competition, although difficult to study and demonstrate in natural communities, is responsible for niche-diversification resulting in the apparent complex structure seen in some communities. Others (e.g., Dayton et al., 1974) implicate predation as the driving force

responsible for maintaining structure. Menge and Sutherland (1976) suggested that competition and predation are complementary. They predict that competition will be the most important organizing mechanism in trophically simple communities while predation will be the primary mechanism in trophically complex communities.

Neither of these questions, similarity or structure, are common in the helminthology literature but both have been addressed to some extent.

One of the basic tenets held by most helminthologists is that individual hosts of the same species tend to be more similar to each other, with respect to their helminths, than to individuals of another species (Auer, 1951; Dogiel, 1964; Noble and Noble, 1974). Acknowledging this tenet, similarity questions became more interesting when related and/or ecologically similar hosts were found to share some of the same species of helminths, or when the same host species, sampled at different parts of its geographical distribution, exhibited little similarity in helminth faunas (Dogiel, 1964).

Perhaps the first to take a holistic, community approach and to quantify their observations were Holmes and Podesta (1968). They found the helminths of wolves to be basically similar over a wide geographical range while the helminths of coyotes varied extensively between regions. Their analyses suggested that observed distributions of helminths across these host species were explicable by the

respective host's food habits. This quantitative, community approach to similarity has been followed by some recent authors (e.g., Pence and Sell, 1979, comparing helminth faunas of greater and lesser prairie chickens, Tympanuchus cupido and T. pallidicinctus). Unfortunately, others, addressing what should be identical questions, have provided little more than species lists coupled with prevalence (e.g., Bush and Forrester, 1975, comparing helminth faunas between different populations of white ibis, Eudocimus albus). In short, although many helminthological studies provide ample data to address questions related to similarity or dissimilarity of faunas, few take advantage of those data and an even smaller proportion of those attempt to quantify their results.

Structural questions are also inherent in many helminthological studies but authors seem to focus primarily on an individual species' predilection for choosing a specific intermediate host or a particular location within the definitive host. In effect, the questions are again concerned with habitat selection and few authors consider the synthesis of more than one individuals' niche preference into a community matrix, thus negating subsequent community analyses.

Organizational questions have been recognized, however (summarized in Hair, 1975), and have recently led to four divergent views of community structure in helminths. Rohde (1977, 1979, and references therein) suggests that the

likely reason for niche restriction is to increase intraspecific contact thereby facilitating mating. Price (1980) suggests independent colonization by specialists adapted to different habitats. Brooks (1980) advanced the hypothesis that helminth communities were simply coevolved units with no interaction in descendant communities. None of these authors consider interactions between species as important organizing forces. Holmes (1973) and Hair and Holmes (1975) suggest that niche restriction is due to biotic interactions; the inference is that these communities are mature and that niche restriction is a mechanism to avoid competition.

Although some helminthologists have addressed community questions, none have extolled the benefits of their systems for ecological analyses. Helminth communities, especially communities of intestinal helminths, have four major features which make them an interesting alternative to the commonly-used freeliving assemblages with which to investigate questions on community similarity and structure. First and most important, is that they are confined to a single host individual, which provides unambiguous boundaries within which interactions between helminth species are complete. The assemblage of helminth species in each host can be considered an intracommunity, in a sense analogous to the use of infrapopulation for the population of a given helminth species in an individual host (Esch et al., 1975). Second, since each host individual provides a

separate, independent infracommunity. Infracommunities are easily replicated and features of structure or similarity can be investigated statistically. Third, one of the truly unique features in these systems is the complete lack of predation on, or by, helminths within the host intestine. If Menge and Sutherland (1976) are correct, this should increase the importance of competition as an organizing force. Fourth, a final useful feature of the intestinal habitat is that it is a complex gradient, with most of the physical and chemical parameters changing along the length of the intestine, but generally correlated with the location. A single environmental axis therefore provides most of the information about the environment of an intestinal helminth (this concept will be discussed more fully later).

My proposal is to examine intestinal helminth communities of lesser scaup ducks, Aythya affinis (Eyton). Noting that "...there is no such thing as a standard protocol for community analysis" (Jonger and Colwell, 1977), I will address features of the two topics that I have introduced above - similarity between infracommunities and structure within infracommunities. Specifically, my first objective is to look for recurrent groups of helminths within the infracommunities and to examine similarity between infracommunities. My second objective is to examine structure within an average infracommunity using actual infracommunities as replicates, and to look for interactions

important to that structure. I will generate many more questions than I will answer and hope that any conclusions reached are reasonable considering the information available. First, however, I turn to particular features of the system on which my assumptions and conclusions are based.

II. The System

It is not my intent to furnish a comprehensive review of avian biology nor helminth physiology. Rather, because of the unusual system, I simply attempt a brief overview of the salient or unusual features, limited to factors important in determining the nature of the community.

An Abundant And Motile Habitat

Lesser scaup are considered to be the most common diving duck in continental North America (Palmer, 1976). Bellrose (1978) states that the breeding population averaged 6.9 million between 1955 and 1975 with a low of just over 5 million in 1965 to a high of over 9 million in 1959. The estimated wintering population in the late 1980's was on the order of 4 million (Palmer, 1976). Data collected by the United States Fish and Wildlife Service and made available by the Canadian Wildlife Service indicates the estimated lesser scaup population in Alberta in 1976 was over 1.7 million.

Lesser scaup breed throughout the Canadian Prairies and the northern United States. They winter principally along the Atlantic and Pacific coasts of North America and the coastal plains of the southern United States. Although the precise migratory corridors are unknown (Palmer, 1976), 40% of the lesser scaup wintering in Maryland, 29% of those in New England, 21% of those in Louisiana, 30% of those in

Texas, and 27% of those wintering in California originate in Alberta (Bellrose, 1976).

Breeding birds are seasonally resident, males until the females are well-into incubation, females until several weeks post-hatching (Trauger, 1971; personal observation). Surplus males and most non-breeding females (generally those under age two) raft together and move between water bodies (Trauger, 1971). Lesser scaup undergo a post-nuptial molt (July to August for males, early fall for females) rendering them flightless for a period of at least 3 weeks (Palmer, 1976). This confines them to a particular lake much the same as if they were breeding birds. Thus, male birds still in pair bonds, female birds brooding, and non-flying moulting birds are on a lake a sufficient length of time to be considered residents. As such, their helminth communities should reflect the dynamics of lesser scaup helminths in that lake. Lesser scaup constitute an abundant and motile habitat, but selection of seasonally resident birds can minimize the problems associated with that motility.

A Single Resource Axis

The gastrointestinal tract is, without question, the most favored site for adult helminths (Mettrick and Podesta, 1974). I have focused my attention on the helminths found in the intestinal tract of lesser scaup. My area of attention is a discrete unit, beginning with the proximal end of the

small intestine and ending with the distal end of the large intestine. It has three obvious and distinct habitats: the small intestine, the large intestine and the ceca. Ecotones between these habitats are narrow or absent.

The small intestine is essentially an aquatic environment (Crompton, 1970) with little turbulence (Crompton, 1973). In mammals, there is a gradient of proteins, amino acids, and carbohydrates along the small intestine (Mettrick, 1971). Although this has not been as carefully documented, data in Crompton (1969, 1970) suggest a similar gradient in ducks. Predictable differences in mucosal morphology occur, such as the change in size and number of villi along the intestine (Crompton, 1973). The overall constancy and predictability of properties along the intestinal gradient are features stressed in the reviews by Crompton (1973) and Mettrick and Podesta (1974). The small intestine is generally considered homeostatic by Read (1971) although Hopkins (1969) and Crompton (1970) suggest that it may be more stable in the posterior portion than in the anterior. Rogers (1962), considering the general concept of the alimentary canal as an environment, suggests that the physico-chemical properties vary not only along the length of the gut but with the distance from the mucosa as well.

The ceca of ducks are of the intestinal type (i.e., containing intestinal materials), and presumably have a role in digestion (Ziswiler and Farner, 1972). The large intestine functions primarily in water resorption and in

temporary storage of intestinal contents, with no apparent role in digestion (Ziswiler and Farner, 1972).

The intestinal tract represents a single resource axis; the small intestine is a complex gradient, characterized by clines of physico-chemical properties, while the large intestine and ceca are relatively homogeneous.

Populating the Host - Immigration and Death

With rare exception, the species comprising the helminth community in lesser scaup are acquired by ingestion of an infected intermediate host. It seems intuitively obvious, therefore, that the food habits of lesser scaup are of fundamental importance to the development of the helminth community. Early reports on the feeding ecology of lesser scaup (Bent, 1923; Cottam, 1939) suggested that they are chiefly vegetarian. Although Rogers and Korschgen (1966) reported traces of vegetable material in all birds examined, they concluded that animal material is the most important food source (see also the summary in Palmer, 1976). There seems little doubt that invertebrates, principally amphipods, are the most important food on the breeding ground (Rogers and Korschgen, 1966; Johnsgard, 1975; 1979). Not surprising, Graham (1956), Denny (1969), Podesta and Holmes (1970a, 1970b), and Hair (1975) found that the dominant helminths of lesser scaup on Cooking and Hastings Lakes, Alberta, cycled through Gammarus lacustris or

Hyalella azteca, two locally abundant amphipods.

For such helminths which are passively transported to the host, chance is an important component in reaching a host and contributing to the helminth community. The legendary high reproductive potential of many helminths has often been considered an adaptation of these helminth species to enhance the odds for survival (but see Jennings and Calow, 1975 for an alternative view). Recent studies in both terrestrial and aquatic systems suggest that some intermediate stages may alter the intermediate hosts' behavior resulting in enhanced predation (see review in Holmes and Bethel, 1972). Facilitated transfer by the helminths infecting lesser scaup has not been tested and it is not known to what extent, if any, the lesser scaup helminth community is selectively populated.

None of the intestinal helminths of scaup is known to reproduce in situ; increases in the fauna are strictly through immigration of new larval stages. On the other hand, once excysted in lesser scaup, the helminths cannot move or migrate between birds. In effect, emigration equals death.

In summary, the helminth assemblages observed in the birds sampled reflect the balance of immigration and death, with immigration a function of the feeding ecology of lesser scaup, perhaps enhanced by facilitated transfer.

The Intestinal Guilds

My analysis, limited to helminths, includes representatives from the Trematoda, Cestoda, Acanthocephala, and Nematoda. I consider all of the intestinal metazoa, in my system, to collectively form three distinct feeding guilds (sensu Root, 1967) in that, regardless of taxonomic position, they exploit the same class of environmental resource by a similar fashion within each guild.

Trematodes have a well-differentiated gut and are generally considered to be grazers, feeding indiscriminately on host tissue and/or blood and on intestinal contents (Rogers, 1962). Recent evidence (Erasmus, 1972; Pappas and Read, 1975) suggests that a surprising amount of nutrient uptake occurs through the body wall, much as in cestodes and acanthocephalans. The latter two groups lack a differentiated gut and all are true absorbers. Nutrients, consisting of small molecules from the intestinal contents or host secretions, are absorbed across the body wall (Rogers, 1962; Crompton, 1973). Nematodes have a well-differentiated gut and feed on blood and/or tissue of the host or on intestinal contents (Rogers, 1962). Their cuticular covering appears to be impervious to nutrient uptake (Rogers, 1962). Thus there are four diverse groups of metazoans feeding on essentially the same products by somewhat different mechanisms: the strict absorbers lacking a gut (cestodes and acanthocephalans), the strict engorgers possessing a well-differentiated gut and incapable of

absorbing across the body wall (nematodes), and the intermediary, indiscriminately, engulfing and occasionally absorbing trematodes.

I conclude that the fundamental unit of this system is a trophically simple complex, composed of three distinct guilds of helminths: the indiscriminate, engulfing trematodes, the absorbing cestodes and acanthocephalans, and the discriminate, engulfing nematode.

III. Study Areas

Collections were made from lakes in three of the four biomes of Alberta (Figure 1). Omitted was the foothill-mountains biome, where lesser scaup do not breed regularly and are mostly transients. Selection of lakes was made with an attempt at maximizing variability (both abiotic and biotic) within each of the three remaining biomes.

The southeast portion of Alberta is an arid short grass prairie. Permanent water bodies are rare; those that persist are generally man-made reservoirs. Four lakes in the short grass prairie were sampled. All were man-made and all had essentially similar surrounding land-use: predominantly pasture with a moderate degree of cultivation. Trees were typically absent, when present they were planted windbreaks of shrub willows (Salix spp.) along scattered sections of the shore.

Aspen parkland covers a band in the south-central region of Alberta, widest along the eastern boundary and narrowing as it approaches the foothills in the west. The parkland effectively provides a transitional ecotone between the prairie to the south and the boreal forest to the north. Traditionally, it was an area of alternating aspen groves and grassland although most of it is now in cultivation or pasture. It is characterized by large, shallow lakes, small sloughs, and ponds. Four lakes in the aspen parkland were sampled, all were extremely shallow, each with an average depth of less than a meter. All had a belt of typical aspen

Figure 1. Sample Lakes in Alberta. 1=Prairie, 2=Aspen
Parkland, 3=Boreal Forest, 4=Montane. Half
circles=1976, Solid circles=1977, Open squares=
1978, Solid squares=1977 and 1978.

parkland along the shore varying from a minimum of 10% of the shore at Fleetinghorse to a maximum of 50% at Dusty. The remaining shoreline was either in pasture or in cultivated fields.

Most of Alberta is boreal forest. This area is characterized by a profusion of lakes, ponds, sloughs, and muskeg, generally differing from the parkland in having deeper lakes and permanent small bodies of water. Five lakes in the boreal forest were sampled. All were relatively large and each had an average depth of at least 3 meters. Three of the lakes (Iosegun, Wolf, and Bistcho) were completely surrounded by boreal forest, the remaining two (Charron and Chip) had 80 and 70% of the shoreline in boreal forest respectively. The area on Charron and Chip not covered by forest was in either pasture or cultivation.

Selected abiotic features for each lake are presented in Table 1.

Table 1. Summary of abiotic features of 13 Alberta lakes surveyed during 1976, 1977, and 1978.

	Area (hectares)	Shoreline (km)	Average depth (m)	Maximum depth (m)
<u>BIOME</u>				
<u>Prairie</u>				
Rattlesnake	157	16.4	5.1	16.3
Murray	1730	34.1	1.8	6.9
Tyrrell	393	14.2	4.0	5.4
Cowoki	917	22.4	1.5	6.6
<u>Parkland</u>				
Lanes	760	26.9	<1*	1*
Dusty	393	12.0	<1*	1.5*
Bellshill	367	11.2	<1*	1*
Fleeinghorse	285	13.0	<1*	1.1
<u>Boreal</u>				
Iosegun	932	17.8	4.6	10.7
Chip	7519	52.8	3*	5*
Charron	838	35.8	3.6	5.4
Wolf	233	8.1	4.2	5.9
Bistcho	41396	164.8	3.6	6.9

* No data available; estimates based on observations during current study.

IV. Methods and Materials

Helminthology

A total of 45 birds was collected from 13 lakes during the breeding seasons of 1976-1978. Collections were initiated on the southernmost lakes in mid-May and progressed northward until the northernmost lake was sampled in late July-early August. This design followed the breeding chronology of lesser scaup and allowed the collection of resident birds on each lake. Breeding females were collected in priority over other birds, followed by mated males and, as a last resort, moulting birds. All birds used in the present analyses were either breeding females or their mates, with the exception of one male from Bellishill Lake that was part of a trio and one male moulter from Bischo Lake. All birds from each individual lake were collected within a two day period and, on the larger lakes, all were collected within the same general region.

Within five minutes of death, the intestinal tract was isolated by tying at the junctions of the gizzard-small intestine and cloaca-large intestine. The tract was removed from the carcass and arranged in the bottom of an enamel pan so that no portions of the tract overlapped. The pan was then flooded with absolute ethanol which had been chilled to approximately -70C by saturating the alcohol with blocks of dry ice. The intestinal tract, effectively frozen in less than 30 seconds, was placed in a plastic bag, sealed, and removed to a cooler with dry ice. The intestinal tract

remained frozen until subsequent examination. This rapid freezing ensured that not only would the helminths be preserved, but there would be no opportunity for post-mortem migration of the helminths.

In the laboratory, the small intestine was partially thawed, straightened, and cut into twenty equal sections. Each section of the small intestine, the large intestine, and each cecum was placed in an individually numbered 8 dram vial and returned to the freezer. At the time of examination, each section of the small intestine was individually thawed in saline. The contents were expelled, the large worms were removed, and the intestinal contents were gently homogenized in the saline. The section was then split longitudinally, placed serosal surface up in a petri dish with saline, and this surface was then scraped. This procedure removed those helminths in intimate contact with the intestine yet did not damage the specimens.

The exceptionally large number of helminths frequently encountered in individual intestinal sections necessitated using a dilution technique. When more than 500 helminths were found in a section, the long or heavy bodied helminths were removed and counted individually; the remaining helminths and intestinal contents were poured into a 100ml graduated cylinder. Saline was added to the cylinder to bring the level to 100ml, the cylinder was inverted several times, and the contents were allowed to settle. The supernatant was decanted and the process repeated until the

supernatant was clear. The supernatant from all sections in the first 10 birds examined was searched for helminths. None were found. This procedure facilitated helminth recovery by removing intestinal mucosa and detritus. Following this procedure, saline was again added until the solution equalled 100ml, the cylinder was inverted four times, and 10ml of mixed solution was decanted into a petri dish. All helminths in this 10ml subsample were counted and identified. A second 10ml sample of mixed solution was decanted and the helminths in this subsample were counted and identified. The results of the two subsamples were compared. If the abundances of the most common helminths differed by more than 15% (approximately 1% of the cases), a third subsample was counted. This procedure was repeated until two subsamples were in agreement. The sum of the helminths in the two samples was then multiplied by 5 as an estimate of total abundance, by species, in that section.

Helminths were identified in temporary water mounts using a compound, phase-contrast microscope at 600X magnification. Permanent preparations were made using standard techniques and a variety of stains. However, these preparations were found to be inadequate for identification of the many species of small hymenolepid cestodes without prior knowledge of internal anatomy obtained from temporary water mounts. Nematodes and acanthocephala were identified as temporary mounts, cleared in a 1:1 mixture of lactophenol and beechwood creosote.

Estimates of Lake Biota

Although time constraints did not permit a comprehensive biological survey at each lake, attempts were made to obtain semi-quantitative estimates of invertebrates and fish. Invertebrate samples were obtained from dip net samples taken in vegetated areas both along shore and offshore. The number of samples taken was in an inverse proportion to the number of amphipods obtained, the fewer the number of amphipods in initial samples, the more extensive the sampling effort. Invertebrates were also collected in seine samples taken in vegetated areas along shores and in a dredge sample of approximately 2 meters taken offshore in deep water. Fish samples were obtained from seines, gill nets, and minnow traps. Seine samples were taken along shores, in both vegetated and open areas; the maximum depth sampled in each lake was approximately 1 meter. A single gang of gill nets, composed of 45 meters each of 2.5, 5, 7.5, and 10 cm mesh, was set overnight for a single night on each lake with the exception of stocked lakes or those supporting commercial fishing. Nets were not set in parkland lakes due to their very shallow nature. Two minnow traps were set each night for 3 nights. In lakes where gill nets were set, the traps were attached to the gang of gill nets for one overnight set; on the remaining two nights, and all 3 nights on other lakes, the traps were set in shallow water. Table 2 presents semi-quantitative data on invertebrate collections and fish collections for

Table 2. Summary of biota collected from 13 Alberta Lakes. Values range from 0 (absent in samples) to +++ (very abundant). Zero does not presume absence, rather, the organisms were not collected in the samples but may have been present in low numbers.

BIOME	Invertebrates					Fish	
	Amphipods	Gastropods	Pelecypods	Chironomids	Other	Forage	Benthic
<u>Prairie</u>							
Rattlesnake	0	+	0	+	+++	yes	yes
Murray	++	++	++	+	0	no	yes
Tyrrell	++	+	0	+	0	no	yes
Cowoki	++++	++	0	0	0	yes	yes
<u>Parkland</u>							
Lanes	+++	+	++	++	+++	no	no
Dusty	+++	+	0	+	++	yes	no
Bellsnail	+	+	0	+++	+	yes	no
Fleetinghorse	0-+++	+	0	+++	+++	yes	no

Table 2 (continued)

BIOME	<u>Invertebrates</u>					<u>Fish</u>		
	Amphipods	Gastropods	Pelecypods	Chironomids	Other	Forage	Predatory	Benthic
<u>Boreal</u>								
Iosegun	+++	++	****	****	****	yes	yes	yes
Chip	++++	++	0	0	+#	no	yes	yes
Charron	++	++++	++++	++	+++#+	yes	yes	yes
Wolf	++	++++	+++	+	+#	no	yes	no
Bistcho	++	+	+++	++	++*	yes	yes	yes

* Back swimmers

** Only present in streams and along shore near stream inlet.

*** Branchinecta

**** Not sampled

Insect larvae

Caddice-fly larvae

each lake sampled.

Estimates of waterbird populations were made from replicate transect counts conducted at the same time on two consecutive mornings. Counts were made from a 19 foot freighter canoe (inflatable Zodiac on fly-in lakes) equipped with an outboard motor moving at approximately 5 - 7 km/hr. Each morning, a transect was run along shore, through weed beds when encountered, for approximately 2 - 3 km. In those lakes where waterbirds were rare, the entire lake shore was counted. When the shore transect was completed, an open water transect was conducted. On smaller lakes, the largest expanse of open water was surveyed; on large lakes, approximately 2 - 3 km were surveyed. The same transects were surveyed a second morning and the results of the surveys were averaged to determine the number of each species of bird per kilometer on each lake. Occasionally, later work on a lake revealed the presence of a species not detected during the initial survey or a greater abundance of a species than suggested by the transect. In these cases, the rank of abundance of each bird was subjectively re-evaluated to reflect the additional information. Tables 3 and 4 present comparisons between lakes based on the numerical abundances and on subjective ranks respectively.

Analytical Methods

This brief section includes general methods pertinent

Table 3. Abundance of dominant groups of birds by lake. Expressed as number of birds/kilometer. Based on raw counts.

	Arctic				Parliament				Boreal				
	RS1	RS*	MU	TY	LA	DU	BL	FH	IS**	CP	CH	WF	B0
Looniformes													
Divers	0.44	0.26	12.18	20.42	50.12	14.72	45.83	8.99		56.97	52.23	1.66	20.57
Cabblers	8.72	7.41	50.0	12.13	28.81	30.22	8.58	20.21		25.86	10.28	1.3	4.34
Canada Geese	0.17	0.43	3.9	0.0	1.17	0.06	0.14	0.0		0.42	0.0	0.0	0.0
Mergansers	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.02
Total	9.3	8.10	66.08	32.55	80.10	45.41	54.55	29.20		83.27	62.46	2.96	23.26
Podicipediformes													
Total	0.7	0.99	47.07	36.70	3.83	1.65	75.81	1.40		1.37	26.91	0.85	1.40

Table 3. (continued)

	Fraser				Parkland				Boreal				
	RS ¹	RS*	MU	TY	LA	DU	BL	FH	IS**	CP	CH	WF	BO
Others													
Coots	0.60	0.0	0.0	12.73	10.35	29.49	5.29	0.0		32.87	1.42	0.0	0.0
Loons	0.0	0.0	0.0	0.22	0.0	0.0	0.0	0.0		0.0	0.09	0.12	0.08
Gulls	0.09	0.95	1.68	18.76	0.52	0.06	0.55	0.84		0.16	6.16	0.0	0.13

RS=Redpoll, RS*=Redpoll, MU=Myrtil, TY=Tyto, LA=Lanes, DU=Dusty, BL=Bellshill, FH=Fleeinghorse, IS=Isosyn.

CP=Cherry, CH=Cherry, WF=Wolf, BO=Blackbird.

* Data collected from Patterson Lake

** Data not collected for Iosegun Lake

Table 4. Comparative abundances of water birds on 13 Alberta lakes. Ranks include only the six most abundant species and range from 1 (most abundant) to 6 (least abundant).

	Prairie						Parkland						Boreal					
	RS*	RS	MU	TY	CK		LA	DU	BL	FH			IS	CP	CH	WF	BO	
	78	78																
Divers																		
Lesser Scaup	5	4	3	4	1		1	4		2			3	6	4	4	2	
White-winged Scoter					3					4				2		1	1	
Ruddy Duck							1		3									
Bufflehead									4				2		2			
Goldeneye													1	4		6		
Canvasback																	6	
Redhead																		6

Table 4. (continued)

	Prairie					Parkland				Boreal				
	RS	RS	MU	TY	CK	LA	DU	BL	PH	IS	CP	CH	WF	BO
<u>Dabblers</u>														
Mallard	4	1	4		4			5	1	4	5		5	4
Blue-winged Teal		5	6	5	5	5	2	6		5	3			
Green-winged Teal						2								
Widgeon	3								5			6		5
Gadwall							5		3					
Pintail	2	2	2											
Shoveler		3	5	6										
<u>Other</u>														
Canada goose	6													

Table 4. (continued)

	Prairie					Parkland				Boreal				
	RS*	RS	MU	TY	CK	LA	DU	BL	PH	IS	CP	CH	WF	BO
	77	78												
Non-anseriformes														
Eared Grebe	4		1	1		6	3	1	6					
Western Grebe												5	3	
Red-necked Grebe												3	2	
Coot				3	2	3	1	2		1	1			3
Franklin's Gull				2										

*RS=Rattlesnake, MU=Murray, TY=Tyrrell, CK=Cowoki, LA=Ianes, DU=Dusty, BL=Bellshill,

FH=Fleeinghorse, IS=Iosegun, CP=Chip, CH=Charron, WF=Wolf, BO=Bistcho

to most of the thesis. Specific methods and their interpretation are important in later sections and will be discussed when first used.

The large size of my dataset required some form of summarizing statistics. Using individual birds as replicates, I chose to use means, standard deviations, and ranges for that purpose. For describing the distribution of a population along a gradient, I used the location of the median individual and the anterior and posterior end points of that distribution. Since each intestine was divided into 20 equal sections, and since the exact location of a population's first or last individual within a section could not be determined, the populations were assumed to begin and end in the middle of the first and last sections of occurrence respectively. This allows a maximum of a 2 1/2% error of exact location.

Testing for normality within the dataset was difficult. I attempted using the Kolmogorov-Smirnov statistic and measures of skewness and kurtosis. The results from any of these tests were inconsistent and difficult to interpret. For example, how far can observed values deviate from zero when testing skewness and/or kurtosis and still be considered reasonably normal? For that reason, all results were tested with the appropriate non-parametric statistics.

All general analyses were done using the programs in MIDAS (Fox and Guire, 1976). Cluster analyses were done using Clustan (Wishart, 1978). Clustan will not read data

files from MIDAS, but will read SPSS files. SPSS will read MIDAS files; therefore, SPSS was used as an interface between the two systems. No analyses were performed with SPSS. Unless stated otherwise, 5% was used as the acceptable level of significance for all tests.

Finally, noting Connor and Simberloff's (1979) admonition "You can't falsify ecological hypotheses without data", I include in Appendix 1, a complete intestinal data matrix for each bird used in this study. From these matrices, all of the data presented in the following analyses can be generated.

V. The Helminth Fauna

Forty-five birds were examined, three from each lake except Fleeinghorse and Rattlesnake. The initial three birds collected from Fleeinghorse were unique in their overall low number of helminths and an additional three birds were collected and examined. Three birds were sampled from Rattlesnake in each of two successive years, 1977 and 1978. Attempts to get replicate samples for other lakes in 1978 were thwarted by lack of birds or exceptionally low water levels, making collection impossible.

Summed across all host individuals, a total of 59 species of intestinal helminths, representing over one million individuals, was found. At the individual host level, there was a mean of 22,231 individual helminths per bird (s.d.=24,816; range=81 to 108,477) and a mean of 14 helminth species per bird (s.d.=4; range=8 to 28). Seventeen species were singletons, occurring as single individuals in one bird, all were immature and none could be identified. An additional 13 species occurred in less than 5 birds. Some of these were mature and could be identified, others were immature and identification could not be made. Appendix 2 provides available taxonomic data for these 30 species. For most purposes, except where noted, the dataset has been reduced by eliminating these 30 species.

Table 5 presents data on frequency and abundance for all species occurring in five or more hosts. Several clarifications are necessary. The only identifications made

Table 5. Intraintestinal distributions (mean \pm SD) of helminth species from 45

adult lesser scaup. Only species occurring in five or more birds included.*†

Helminth species	n	N	Median point	End points of distribution	Range
<u>Fimbraria fasciolaris</u>	40	98 \pm 151	11 \pm 3	0 - 23 \pm 7	23 \pm 8
<u>Hymenolepis sp. 2.</u>	6	109 \pm 138	15 \pm 3	7 \pm 9 - 23 \pm 6	17 \pm 10
<u>Echinoparyphium recurvatum</u>	19	75 \pm 179	18 \pm 9	5 \pm 9 - 28 \pm 15	23 \pm 17
<u>Unciunia n.sp.</u>	12	119 \pm 227	19 \pm 12	7 \pm 14- 29 \pm 16	22 \pm 16
<u>Hymenolepis macroskrjabini</u>	17	319 \pm 531	31 \pm 10	15 \pm 12- 37 \pm 11	22 \pm 13
<u>Apatemon gracilis</u>	38	52 \pm 119	27 \pm 10	8 \pm 11- 42 \pm 15	33 \pm 18
<u>Lateriporus skrjabini</u>	22	33 \pm 61	28 \pm 7	17 \pm 9 - 36 \pm 13	19 \pm 18
<u>H. recurvata</u>	23	206 \pm 335	26 \pm 7	10 \pm 10- 39 \pm 12	29 \pm 14
<u>H. melanittae</u>	5	27 \pm 32	34 \pm 10	27 \pm 12- 39 \pm 6	10 \pm 7
<u>Retinometra cyrtoides</u>	7	51 \pm 95	35 \pm 13	23 \pm 13- 41 \pm 13	19 \pm 15
<u>R. pittalugai</u>	32	183 \pm 491	43 \pm 8	26 \pm 12- 51 \pm 14	25 \pm 19
<u>Capillaria pinnatifida</u>	10	177	44 \pm 16	24 \pm 12- 64 \pm 17	44 \pm 16

Table 5. (continued)

Helminth species	n	N	Median point	End points of distribution	Range
<u>Hymenolepis</u> sp. l.	7	85±176	44±9	33±13- 46±9	14±9
<u>H. spinocirrosa</u>	43	7868±10177	45±7	16±15- 57±6	41±15
"O"	5	4±2	46±12	41±12- 48±14	7±4
<u>H. tuvensis</u>	40	1590±1996	54±8	34±12- 68±14	34±16
<u>Oligorchis</u> n.sp.	6	15±14	54±16	43±11- 64±13	22±19
<u>H. abortiva</u>	43	6690±8697	64±6	49±8 - 79±9	30±11
<u>Cotylurus hebraicus</u>	19	17±27	68±10	56±16- 72±17	17±16
<u>H. arcuata</u>	9	26±56	65±10	56±7 - 68±11	12±9
<u>Polymorphus marilis</u>	42	35±61	70±6	55±7 - 82±9	27±11
<u>Tuvenis</u> A	27	2194±3692	71±8	57±11- 87±7	30±11
<u>Corynosoma constrictum</u>	15	4±3	76±8	68±9 - 78±9	11±8
<u>Diorchis inflata</u>	5	7±5	77±6	68±4 - 82±6	14±7
<u>Diorchis</u> n.sp.	8	95±134	77±11	66±15- 88±10	22±15

Table 5. (continued)

Helminth species	n	N	Median point	End points of distribution	Range
<u>Dicranotaenia coronula</u>	23	19±15	83±13	70±19- 90±20	24±17
<u>Diorchis excentricus</u>	10	86±150	85±10	74±9 - 90±10	16±9
<u>H. pusilla</u>	44	4811±6541	90±5	71±8 -100±2	30±9

* Ligocystyle lunata, a trematode found in more than five birds, was restricted to the cecae and is not included in this table.

Species are listed sequentially by order of the median point.

with confidence are those that were described from North America. Species originally described from Europe and Asia in fact, may not be those species. Denny (1969) found slight, but consistent, differences between specimens he called H. tuvensis and the original description. In the current study, none of the species matched the original descriptions exactly, but all were very close; there appear to be sibling species in North America. This has no bearing on the current analyses with the exception of interpreting life cycles of species described in Eurasia. The life cycles of species determined in Eurasia cannot be considered the same in North America unless subsequently verified. For future reference, specimens of all species which were abundant enough to save are deposited in the USNM Helminthology Collection (Nos. 75915-75934) and the University of Alberta Parasitology Collection (hereafter, UAPC) (Nos. 10372-10387).

The community is dominated by the absorber guild, which collectively includes all of the cestodes and acanthocephalans. Over 96% of all the individuals fall into this category. The indiscriminate, engulfing guild is a distant second (less than 4%) in numerical abundance and includes four species of trematodes. As noted earlier, absorption across the body wall has been demonstrated for some trematode species and, as such, they may act secondarily as absorbers. Even in these cases however, engulfing appears to be the predominant feeding mechanism

and the distinction between the true absorbers and the trematodes appears justified. A final group is represented by a single species of nematode and accounts for less than one half of one percent of the total individuals. The feeding mechanism of this particular species is unknown, however other intestinal nematodes are generally discriminate feeders, either on the host or on intestinal contents. For the present purposes, Capillaria obsignata is considered to represent the discriminate, engulfing group.

VI. Faunal Similarity

When examining questions on faunal similarity, three features are of interest: 1) the relationships of the species involved, 2) the relationships of the habitats (or hosts), and 3) the relationships between the species and the habitats. In addressing faunal similarity, I use recurrent group analysis (with some added statistical analyses) for 1), cluster analysis for 2), and principal-components and rotated factor analysis for 3).

Recurrent Groups

Lawlor and Smith (1976) suggested that most natural communities are not arbitrary collections of species but are assemblages of species that have existed together a sufficient period of time for each species to adapt, through natural selection, to each other. Presumably, the longer and more frequent the association between species, the greater the degree of co-adaptation. Replicate samples should therefore exhibit a range of patterns from common, co-occurring species with abundant individuals to rare singletons. Fager (1957) considered these co-occurring species as recurrent groups and suggests that these species which are a nearly constant part of each other's environment, may be important in understanding the abundance and distribution of species. Fager (1957) identified the major problem in recurrent group analysis as being the

determination of these groups by a procedure which can be repeated. The most frequent and least frequent species are obvious within a study and can be selected with little difficulty (e.g., Bush, Holmes, and Humphrey, ms). It is the intermediary species which cause concern.

Fager (1957) reviewed the various grouping techniques noting that none had proven satisfactory in general use and suggested a new technique, using an index of affinity and a series of precedence tests to determine recurrent groups within a series of samples. This index is based solely on presence/absence data. In Fager's words "...it seems best to base species groupings upon presence and absence alone and to consider abundance relations within such groupings after they have been determined".

Once the recurrent groups were determined, Fager suggested a variety of tests appropriate to analyzing relationships within groups. Two of these, dominance and correlation, are particularly useful. When applied to species ranks within samples, Kendall's (1955) test of concordance gives a measure on whether the dominance relationships between species are constant over the sample. An F-test can be used to determine the significance of the concordance value. The correlation between species pairs within groups determines whether species abundances vary in concert, independently, or oppositely. Fager suggested the use of Kendall's tau with an associated t-test to determine correlation and the significance of the correlation.

Fager and McGowan (1963) modified the earlier index of affinity to incorporate the geometric mean of the proportion of joint occurrences, corrected for sample size. Hayes (1978) has shown that the Fager index errs on the conservative side and one might place "...considerable confidence in the reality of recurrent species groups that are derived through its application".

Recurrent group analyses have been used successfully for a wide variety of faunas ranging from marine zooplankton (Fager and McGowan, 1963; Venrick, 1971; Rottman, 1978; McGowan and Walker, 1979) to demersal fish (Fager and Longhurst, 1968) and even to plant associations (MacDonald 1975). To my knowledge, this potentially useful technique has not been used as a preliminary screening technique for helminthological data.

Recurrent Groups of Helminths in Lesser Scaup

The index of affinity (Fager and McGowan, 1963) was used to examine affinal relationships between species pairs of intestinal helminths of lesser scaup. Only the 16 most frequently occurring species were used in the analysis because the number of joint occurrences between a rare species and a common species cannot be a significant proportion of the total number of occurrences of the common species. If the rarer species were included in the analysis, one might conclude that they show no affinity with a common

species even though they may always co-occur.

Figure 2 summarizes the meaningful affinities (index of affinity $\geq .5$, Fager, 1957; Fager and McGowan, 1963; Venrick, 1971; Rottman, 1978) between all species pairs for the 16 species used in the analysis. Only one recurrent group, containing 10 species (H. spinocirrosa, E. abortiva, H. pusilla, H. tuvensis, E. fasciolaris, R. pitalugai, C. coronula, P. marilis, A. gracilis, and Tuvensis A) can be formed. This group contains two components: 8 species of hymenolepid cestodes, one acanthocephalan and a trematode. Four of the hymenolepids (and possibly Tuvensis A which never matured and could not be identified with certainty) are closely related members of the subgenus Microsomacanthus. Six of the species H. spinocirrosa, H. abortiva, H. pusilla, H. tuvensis, R. pitalugai and P. marilis are specific to lesser scaup. Tuvensis A, since it never matures, cannot be considered specific to scaup. The remaining three species are widespread generalists. The remaining six of the 16 species originally used in the analysis are all associates of this group, showing significant affinities to all (or most) of the recurrent group members, but not to each other. These associate species do not form secondary groupings.

Kendall's (1955) coefficient of concordance suggests the relative abundances between the species in the recurrent group tend to be constant over the samples ($p < .001$). Unfortunately, this test can only be applied to those

Figure 2. Trellis diagram of the 16 most frequent species used to test for recurrent groups. An "X" indicates a species pair with an index of affinity ≥ 0.5 . Species arranged by frequency of occurrence.

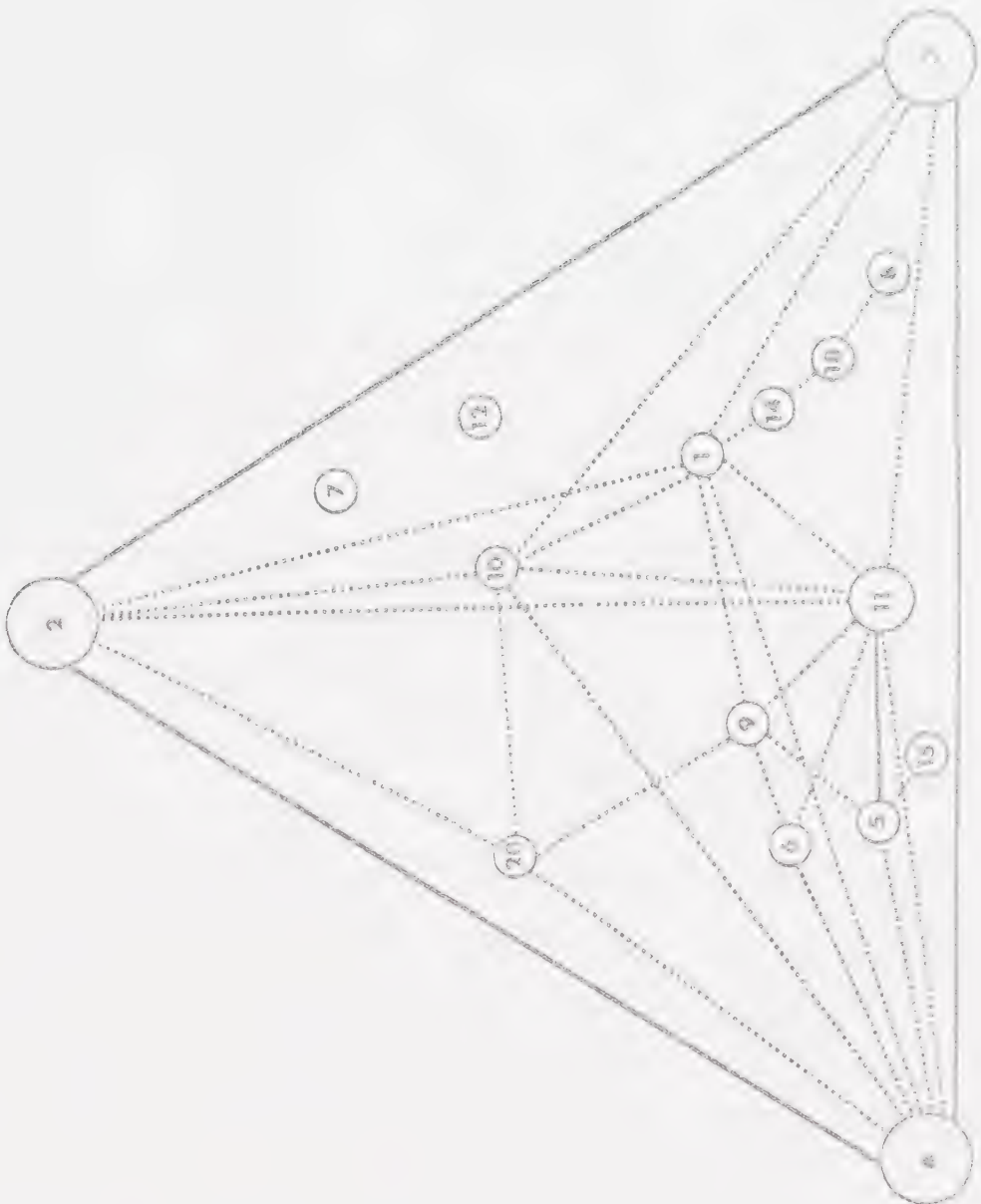
samples in which all ten species co-occur (9 of 45).

Therefore, it seems more informative to examine pairwise rank correlations to define relationships between species.

Paired rank correlations (Kendall's tau) were examined between all possible pair combinations (105 pairs) of the 16 species used to test for recurrent groups. All of the correlations were positive. That there were no negative correlations would indicate that an increase in the abundance of any one species was never associated with a corresponding decrease in abundance of a second species. Further examination of the positively correlated variables seems warranted as they seem to be responding in concert. Thirty-one of the 105 possible combinations, involving 14 species, were significant at $p < .05$ (Figure 3). This suggests that in the majority (74) of the pairwise comparisons, the species abundances vary independently of each other. Figure 4 presents a diagrammatic relationship between the 16 species based on the magnitude of their correlations. Solid interconnecting lines are correlations significant at $p < .0001$, dashed lines represent other significant correlations. Six species in the recurrent group (H. spinocinctosa, H. aboriva, H. pusilla, E. fasciolaris, X. pittalugai, and P. marilis) are not only regularly co-occurring, they are significantly intercorrelated as well. Note that two species, E. recurvatum and D. coronula, are not correlated with any other species. Another four species, A. gracilis, C. hebraicus, H. recurvata, and H.

Figure 3. Trellis diagram of the rank correlations (Kendall's tau) between the abundances of the 16 frequent species. A "*" represents a correlation significant at $p < 0.001$. A "#" represents a correlation significant at $p < 0.01$. A "+" signifies other significant correlations.

Figure 4. Diagram of the intercorrelations of abundance between the 16 frequent species. Solid lines emphasize very highly significant correlations of abundance (Kendall's tau). Dashed lines are highly significant and significant correlations. Species codes are the same as those in the legend for Appendix 1. See text for further discussion.



microskrijabini share at most, correlations with two other species. The remaining species show reasonably good intercorrelations and include two species, L. skrijabini and C. constrictum that are not a part of the recurrent group. Perhaps the most interesting feature of this diagram is the exceptionally high intercorrelation between H. grinnellensis, H. abortiva, and H. pusilla. All possible combinations of these species are correlated at $p < .0001$. Another two species combination, P. marilis and H. tuvensis share this remarkably high correlation. The magnitude of these correlations suggest that there may be an underlying factor, or two factors (one for each group), responsible for these positive correlations.

Fager and McGowan (1963) and Venrick (1971) used multiple regression analysis to examine relationships between members of recurrent groups and the physical environment. Unfortunately, two of the primary assumptions for regression analysis are that the data be normally distributed and that the independent variable be measured without error (Sokal and Rohlf, 1969). Neither of these assumptions are valid with my dataset. Therefore, I have again used rank analysis (Kendall's tau) to examine relationships between the members of the recurrent group and selected features of each lake. Other recent authors (e.g., Rottman, 1978; McGowan and Walker, 1979) have also used rank correlations for this purpose. Since I had three observations on helminths from each lake (six from

Fleeinghorse) and only one series of observations on selected features from each lake, I used mean helminth abundance, by species, as the variables to be examined for correlations. Table 6 presents lake variables used for correlation analysis. Not all of these data were collected at Iosegun Lake and it is not used in the analysis. The inference being suggested here is that some parameters, such as those related to water quality, may influence (positively or negatively) the populations of invertebrates (which are intermediate hosts to the helminths) and, subsequently, the helminth populations. Other parameters, such as the composition and abundance of the avian fauna, may be important in that they might act as additional hosts for the helminth species thus increasing local population levels.

Correlations between abundances of helminth species and the abundances of bird species were very difficult to interpret. For example, the abundance of H. spinocinrosa was positively correlated with the abundance of red-necked grebes (Podiceps grisegena) and goldeneye (Bucephala clangula), and negatively correlated with the abundance of pintails (Anas acuta). This species of helminth has never been reported from these hosts and I cannot interpret the relationships.

The relationship between the remaining parameters and the rank abundances of the recurrent group species are not particularly enlightening either. Because of the overall lack of correlations, I have included correlations

Table 6. Biotic and abiotic variables measured at each lake.

Birds per kilometer	
Mallards	Coots
Pintails	Eared Grebes
Widgeons	Horned Grebes
Gadwalls	Western Grebes
Shovelers	Red-necked Grebes
Blue-winged Teal	Pied-billed Grebes
Green-winged Teal	Common Loons
Lesser Scaup	Double-crested Cormorants
Redheads	Franklin's Gulls
Canvasbacks	White-headed Gulls (includes
White-winged Scoters	unidentifiable gulls)
Ruddy ducks	Bonaparte's Gulls
Buffleheads	total dabblers
Canada Geese	total divers
Goldeneyes	total anseriformes
Lake parameters	
area	conductivity
mean depth	total dissolved solids
maximum depth	hardness
shoreline development factor	oxygen concentration
cultivated shore (%)	phosphate
pasture (%)	nitrogen

Table 6. (continued)

Lake parameters (continued)	
forest (%)	secchi disk reading
pH	
Biotic features - ranked abundances	
gastropods	submerged vegetation
pelecypods	emergent vegetation
amphipods	plankton
insects	predatory fish
chironomids	benthic fish
forage fish	

significant at $p < .10$ as an indication of the trend of the relationships. Even then, there are no constant correlations (Table 7). This may simply mean that the observations made at each lake are not important to the invertebrates, the appropriate observations were not made, or even that the observations made were subsequent to the host becoming infected and are totally unrelated to conditions current at the time the infracommunity was developed. This rationale notwithstanding, there are some correlations that may be of interest. Hymenolepis spinocirrosa, H. abortiva, and H. pusilla are negatively correlated with some parameters usually associated with productivity of a lake (hardness and conductivity) such that high values of these variables indicate a eutrophic system. The correlations suggest that as the lake becomes more eutrophic, the relative abundances of these helminths decreases. Remembering that these three species were highly intercorrelated, eutrophication may be a factor responsible for their apparent relationship. Furthermore, these species were all positively correlated ($p < .1$) with oxygen concentrations. Since oxygen concentrations decrease under eutrophic conditions, oxygen concentrations may in fact be a significant variable.

Persistence Stability of Recurrent Group Species

If recurrent groups represent coevolved species, one might predict that they would show persistence stability

Table 7. Significant correlations (Kendall's tau) between mean abundances of helminths forming the recurrent group and 55 lake variables.

Species	Variable	p < .05	p < .1
<u>Hymenolepis spinocirrosa</u>	conductivity(-)		
	total divers(+)		
	oxygen(+)		
<u>H. abortiva</u>	conductivity(-)		
	hardness(-)		
	oxygen(+)		
	gastropods(+)		
	pasture(+)		
	predatory fish(+)		
<u>H. pusilla</u>	conductivity(-)		
	total divers(+)		
	amphipods(+)		
	oxygen(+)		
	emergent vegetation(+)		

Table 7. (continued)

Species	Variable	
	$p < .05$	$p < .1$
<u>H. tuvensis</u>	amphipods(+)	total divers(+)
	total anseriformes(+)	
<u>Tuvenis A</u>	cultivation(+)	benthic fish(+)
	forest(-)	
	hardness(+)	
<u>Fimbriaria fasciolaris</u>	total anseriformes(+)	
	total dabblers(+)	
	cultivation(+)	
<u>Retinometra pittaluga</u>		total dissolved solids(+)
		conductivity(+)
<u>Dicranotaenia coronula</u>		amphipods(-)

Table 7. (continued)

Species	Variable	p < .05	p < .1
<u>Polymorphus marilis</u>	total divers(+)		
	total anseriformes(+)		
	oxygen(+)		
	emergent vegetation(+)		
<u>Apatemon gracilis</u>	total divers(-)		
	pasture(+)		

(sensu Margalef, 1969). Examination of recurrent groups for persistence stability by repeated long-term sampling has not previously been examined. Data from the current study, in conjunction with published and unpublished records, provide the opportunity for such a test.

The current dataset represents 45 adult lesser scaup collected during the summers of 1976 through 1978 from 13 lakes in Alberta ranging from the Montana border to the Northwest Territories border. Prior to this study are three reports of helminths from lesser scaup in Alberta. Graham (1966) reported 25 species of helminths from 135 adult scaup collected during the summers of 1964 and 1965 at Cooking and Hastings Lakes, Alberta. Hair and Holmes (1975) reported 43 species of helminths from 10 adult scaup taken in 1972 at the same two lakes. Later, Hair (1975) examined 30 adult scaup taken in 1973 and 1974 from the same lakes and reported 30 species of helminths. Hair (1975) summarized these earlier data and noted several compositional differences between the studies. The important differences were the absence of Hymenolepis pusilla, H. recurvata, and H. fausti and the presence of H. parvula in Graham's study, the converse being true for Hair's study. Differences between Hair and Holmes (1975) and Hair (1975) were of a taxonomic nature and were resolved by Hair (1975).

I examined a large number of helminth specimens from lesser scaup deposited in the UAPC by Graham. Specimens identified by Graham as H. abortiva included some H. pusilla

(see UAPC slide # 4361) and those identified as H. parvula included some H. recurvata (see UAPC slide # 2362).

Therefore, these two species were present in lesser scaup at Cooking and Hastings Lakes during the mid-sixties.

Hymenolepis fausti may well have been absent from O'Donoghue's dataset. This species was rare in Hair's (1975) study and even rarer in my study. The required host (sensu Holmes, 1979) for this species appears to be the mallard, Anas platyrhynchos (Butterworth, pers. comm.; Neilson, pers. comm.).

Thus, the available data include concentrated studies on the same system 10 years apart, every type of habitat in which lesser scaup are found in Alberta, and a maximum span of 16 years between the first and last collections (although not on the same lake). Although 10 to 15 years may not be considered a long period of time, the biology of the helminths tends to make that duration more significant. For example, the minimum generation time for H. spinocirrosa, from egg to egg, is 13 days (Podesta and Holmes, 1970b). Thus, in an average summer of 150 days, there may be up to 12 generations of this species in that single season and, over a 10 to 15 year span, up to 120 and 180 generations respectively. With some corrections (see above), nine of the 10 species assigned to the recurrent group have been reported from all four studies on lesser scaup. In comparing the relative abundance among the four studies on adult birds (which might reasonably be considered to represent mature

faunas) Kendall's coefficient of concordance was 0.65 ($p < .001$). This is particularly good concordance considering some of the taxonomic differences. Comparing Hair's (1975) study and the current study, the abundance ($\tau = 0.90$, $p < .0001$) and frequency ($\tau = 0.74$, $p < .05$) of occurrence are reasonably similar.

One species, *Tuvenis A*, is reported only from the current study. That it was never reported from previous studies may simply represent the evolution of increased taxonomic awareness. Most of the differences (both numerical and taxonomic) between the four studies can be attributed to a refinement of techniques. As a host is studied more intensively, the initial investigator has the almost thankless job of determining what is present, with no prior knowledge. Successive investigators tend to rely heavily on the earliest work and have the opportunity to refine techniques and identifications. In fact, each successive study on lesser scaup in Alberta has resulted in an increased species list.

Discussion

Heretofore, recurrent group analysis has been used to compare similarity of faunas between different habitats, the underlying assumption being that each of the different habitats would have its own unique recurrent group. Considering the current dataset, lesser scaup probably represent one of the better natural systems available in which replicates might be considered identical. One might

then predict that there would be a single recurrent group characterizing this habitat unless the habitat varied in response to different environmental parameters such that the habitat (lesser scaup) is less important than are the environmental variables to which it is subjected.

The results of the index of affinity and associated analyses do suggest a single recurrent group composed principally of habitat specialists but also including some extreme generalists. Fager and McGowan (1963) considered the "vitality" of species (presence of all life stages in the sample) as evidence that the species are reproducing in the habitat and infer that this further solidifies their inclusion in a recurrent group. One species *Tuensis A*, is both frequent and abundant yet never matures. It is a frequent member of the other species' environment, so that the latter may evolve in response to it, but it obviously cannot coevolve with them. Therefore, I subjectively remove *Tuensis A*, leaving nine species. This does not mean *Tuensis A* is unimportant. The other recurrent group species do evolve with *Tuensis A* as an integral part of their environment.

The remaining nine species of helminths forming the recurrent group have been reported in studies spanning 16 years and in a wide variety of lakes. This group is truly characteristic of lesser scaup.

For reasons noted above, the disappointing lack of correlations between helminth abundances and

commonly-measured water quality parameters (plus a variety of other variables) must be interpreted with caution. However, with only a single recurrent group, no subsidiary groups, and no negative correlations, one might predict that host habitat features are unimportant. In short, variables of the host habitat do not appear important to the infracommunities.

The remarkably high positive correlations between some members of the group suggests that these species in particular, are responding in concert to some factor(s). The answer may lie in their respective life cycles. It is known that H. spinocirrosa and H. pusilla use Hyalella azteca as an intermediate host (Podesta and Holmes, 1970b) and they have never been found in Gammarus lacustris (unpublished records, University of Alberta). The life cycle of H. abortiva has not been determined locally, however circumstantial evidence in Podesta and Holmes (1970b) suggests that it too uses H. azteca as an intermediate host. The other highly correlated species pair, P. marilis and H. tuvensis, both use G. lacustris as an intermediate host (Denny, 1969) although H. tuvensis may also use H. azteca (Podesta and Holmes, 1970b). The principle food of lesser scaup is amphipods (see above). The high correlations may well reflect large, essentially simultaneous infections, the highly intercorrelated three species subgroup through H. azteca and the two species subgroup through G. lacustris. Although the correlations are not as high as those in the

subgroups discussed above, two species (F. fasciolaris and R. pittalugai) do have high correlations with other group members, particularly some of the subgroup species.

Fimbriaria fasciolaris uses both species of amphipods as an intermediate host (as well as ostracods and copepods).

Evidence in Denny (1969) and Podesta and Holmes (1970b) suggests that H. azteca is the best intermediate host locally. The correlations between this species and two of the H. azteca subgroup are significant at $P < .01$ (Figure 3). The life cycle of R. pittalugai is unknown as are the life cycles for all species of Retinometra.

Two of the associate species, Corynosoma constrictum and L. skrjabini, show good intercorrelations with many of the group members. C. constrictum uses H. azteca as an intermediate host while L. skrjabini uses G. lacustris. If the above argument regarding the two highly correlated subgroups is correct, these two might be "tag-along" species. Figure 4 indicates that Corynosoma constrictum is correlated with two of the three species using H. azteca as an intermediate host (in addition, the correlation with H. abortiva is reasonably good - $p = .063$) and that L. skrjabini is correlated with both P. marilis and H. tuvensis.

Cluster Analysis

Cluster analysis is a multivariate approach to sorting data into groups so that members of any particular group are

more similar to each other than to non members. The development of cluster analysis stems largely from the work of numerical taxonomists attempting to quantitatively assess species relationships (Sokal and Sneath, 1963). In the past, the benefits of this technique have been largely overlooked by community ecologists with the exception of studies on marine bottom communities (Stephenson et al., 1970 and references therein). Stephenson and his co-workers (1970) first comprehensive attempt at numerically identifying communities presents a summary of the difficulties in classifying communities when dealing with a large number of samples, species, and individuals. Stephenson (1972) further elaborates on the use of clustering theory as applied to community ecology. A later paper (Stephenson et al., 1972) analyzes Petersen-type communities with Petersen's original data, applying multivariate clustering techniques to the problem. Their results did show Petersen-type communities although the structure they obtained differed somewhat from the original results.

A recent application of cluster analysis has been an attempt to define guilds within an assemblage of species. This is considered by Stephenson (1972) to represent "inverse" analysis in that the species are grouped by site attributes as opposed to "normal" where sites are grouped by species attributes. Holmes et al. (1979) defined 27 foraging characters as attributes to examine the relationship between 22 insectivorous birds. They used Euclidean distance as a

similarity coefficient and subjected the resulting distance matrix to hierarchical clustering using the maximum method (=complete linkage, Wishart, 1978). Noting that there was no precedent for quantitative separations of guilds, they chose mean Euclidean distance as a cutoff point to separate guilds. To my knowledge, mean Euclidean distance has no *a priori* biological interpretation.

Pianka (pers. comm.) has experimented with single linkage clustering and suggests that food or habitat guilds can be determined with this approach. He defines a guild as a cluster in which the greatest distance between any species pair is less than the distance between any member of that cluster and any other clusters.

These last two examples emphasize one of the major problems in cluster analysis. Wishart (1978) lists 16 different hierarchical fusion techniques each of which may be coupled with up to 40 similarity or dissimilarity coefficients. Thus there is a major decision in choosing an appropriate algorithm and coefficient. Wishart (1978) notes that complete linkage provides tight spherical clusters; however, the results are irregular because the similarity is only determined between two individuals and does not measure group structure. He further notes that single linkage produces chaining (essentially the opposite of complete linkage) which results in large populations not being partitioned. Thus, in the analyses of Holmes et al. (1979) and that advocated by Pianka, the choice of algorithms might

have predetermined the results.

Sokal and Sneath (1963) advocate the average linkage method employed either as a variable-group or pair-group method. Wishart (1978) indicates that this method takes account of group structure, produces spherical clusters and is reasonably well behaved (not subject to inversions). These are all desirable properties of an algorithm in which no a priori results are anticipated.

Presch (1979), continuing the cladism vs. pheneticism controversy current in numerical taxonomy, examined a single dataset with a variety of similarity coefficients and algorithms. He concluded that different combinations applied to the same data yielded different results and thus rejects the use of cluster analysis in numerical taxonomy. Presch's analyses and ensuing arguments are based on the systematist's desire to use high similarity as an indication of close phylogenetic relationships. In the following analysis, I derive neither evolutionary nor statistical inference from cluster analysis. Rather, I use the technique as a means of data reduction with the implication that the resulting dendrogram (see below for definition) depicts the similarity of samples based on relative abundance of helminth species, nothing more.

In using dendrograms to present the results, I follow the definition of Fink (1979) "Dendrogram is used herein as the appellation for a branching diagram describing character distributions".

Clustering of Lakes by Helminth Faunas

Cluster analysis (Wishart, 1978) was used as a sorting technique to examine similarity of helminth faunas between birds (=samples=infracommunities). This is "normal" analysis (Stephenson, 1972) and the abundance of individual helminth species were used as attributes (variables) to examine relationships. The clustering algorithm employed was the group average method (sometimes referred to as the unweighted pair group method or average linkage method) of Sokal and Michener (1958). The measure used to generate the similarity matrix was the product-moment correlation coefficient for continuous data (Wishart, 1978). Prior to running the analyses, the data were transformed ($\log N + 1$) and standardized (value minus mean divided by standard deviation). This reduces bias of the similarity coefficient towards those variables having large variances (Wishart, 1978).

Although Holmes et al. (1979) used mean Euclidean distance to define important clusters, I have chosen to use a correlation coefficient of zero. Since the combination of strategies selected above yields a coefficient that can range from minus one for complete dissimilarity to plus one for complete similarity, zero represents the mid-point and clusters defined at this region contain elements that can be considered 50 per cent similar.

Initially, cluster analysis was applied to the entire dataset (59 variables). Although this includes rare species

and even some singletons, it was felt that these variables might provide an important uniqueness to the resulting clusters. The results obtained by this approach are presented in the form of a dendrogram (Figure 5). At a coefficient of zero, four robust clusters are defined. The first cluster contains no complete lake unit (i.e., in no case do all samples from any particular lake co-occur within that cluster). The remaining three clusters each contain a lake unit. The three samples from Murray and Cowoki Lakes are all in the second cluster and each sample from this lake is more similar to another sample from this lake than it is to a sample from a different lake. The same is true in the third cluster for Rattlesnake 1977 (= RSA on Figure 5) Lake. The fourth cluster contains all six samples from Fleeinghorse Lake; however, they are not necessarily more similar to each other than to samples from other lakes. For example, sample four from Fleeinghorse is more similar to sample one from Bellshill than to any other samples from Fleeinghorse.

Another way of examining the results of a cluster analysis is to examine the final dendrogram and look at pairwise associations. There is little tendency for a given bird to be highly correlated with another bird from the same lake. This is true even when alternative pairs (e.g., in Figure 5, CK1 and CK3 could actually be paired) are considered.

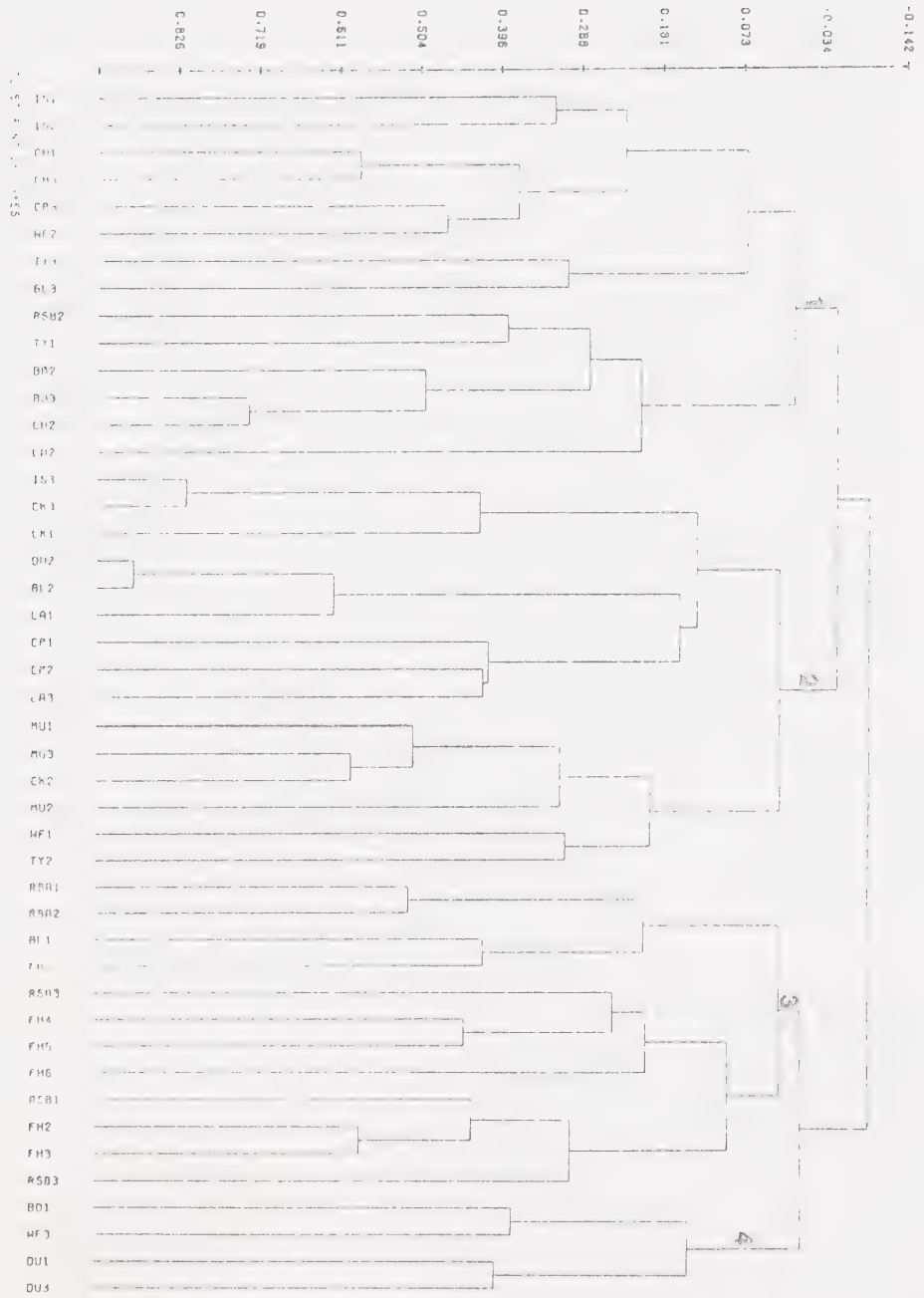
Defined clusters can be used as a priori strata for

Figure 5. Cluster analysis comparing individual birds with respect to the presence and abundance of all 59 helminth species. The vertical axis represents the correlation coefficient. Numbers 1 through 4 on the stem lines delineate the four clusters produced at a similarity of 50%. See text for further discussion.

stepwise multiple discriminant analyses, which determine the most discriminating variables between clusters. At each step, the most discriminating variable is that variable which accounts for the greatest amount of the remaining variance between strata (clusters). In the current analysis, there were nine discriminating variables (helminth species) significant at $p < .05$. There were, in order of significance, H. tuvensis, H. abortiva, Dic. coronula, H. arcuata, H. melanittae, "FF", Capillaria sp., Diorchis n. sp., and (G). In attempting to better understand the structure of the clusters, the variance in mean abundance for the 16 most frequent species (those used in testing for recurrent groups) was examined with a Kruskal-Wallis test (Appendix 3). Note that the most discriminating variable (H. tuvensis) will separate clusters one-two from three-four while the second most discriminating variable will separate cluster one from four. In general, these clusters are separable first by abundant and frequent species, second by rarer, infrequent species.

When the cluster analysis is used to examine similarity with only those species occurring in five or more samples, four clusters are again defined at the zero level (Figure 6). In comparing this dendrogram with the previous one, the results are broadly similar although more complete lake units are formed. As in the previous analysis, all Murray and Cowoki Lake samples occur in the same cluster. Major differences are that all Charron Lake samples are now

Figure 6. Cluster analysis comparing individual birds with respect to the presence and abundance of all helminths occurring in at least 5 birds (29 species). The vertical axis represents the correlation coefficient. Numbers 1 through 4 on the stem lines delineate the four clusters produced at a similarity of 50%. See text for further discussion.



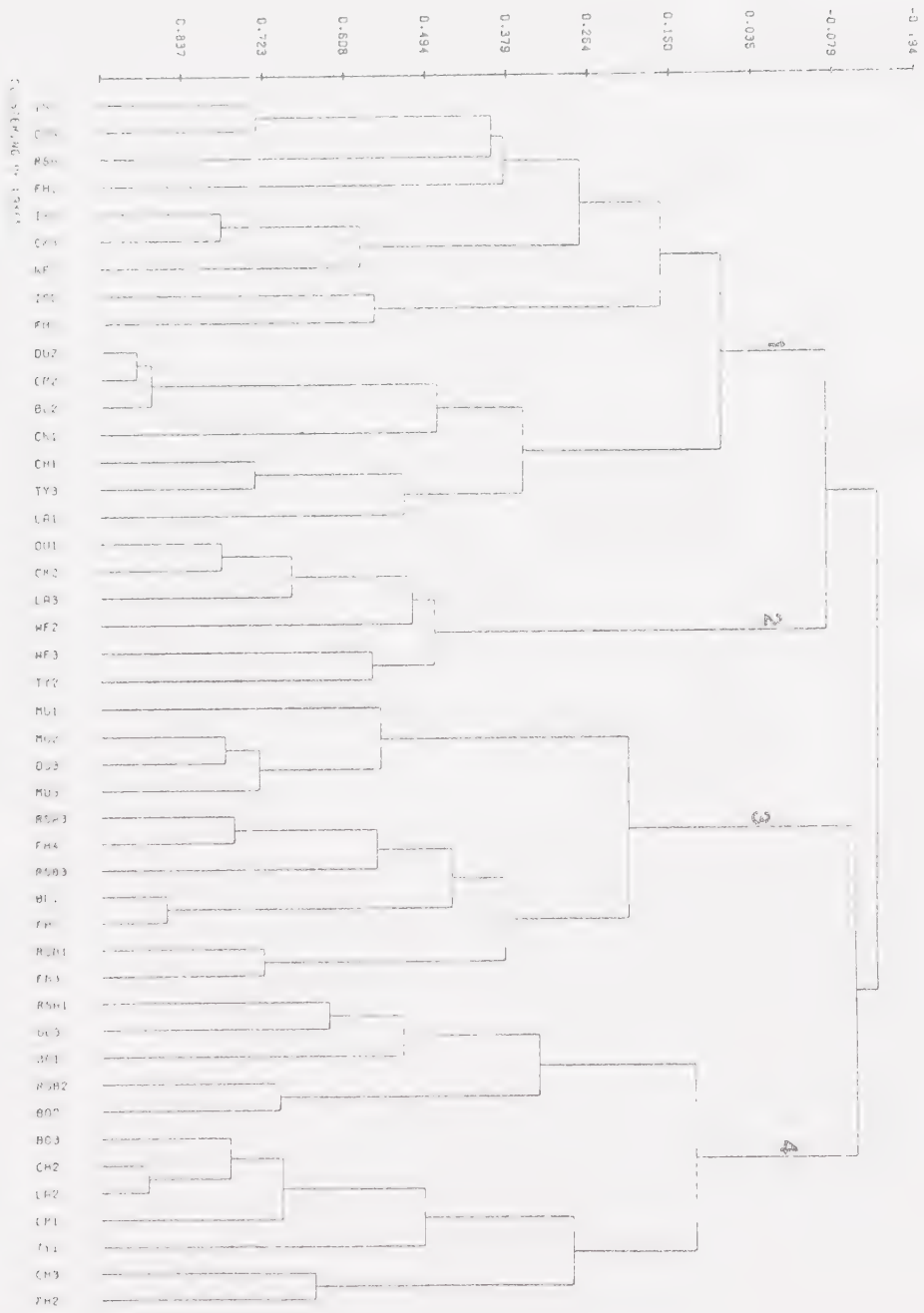
clustered together, and the Rattlesnake (1977) and Fleeinghorse Lake samples now occur in the same cluster.

Examination of pairwise associations shows little tendency for complete lake units to be adjacent (to be compared with two complete sets in the 59 variable dataset). However, there are eight pairs of samples in which two samples from the same lake are more highly correlated to each other than to samples from different lakes (samples one, two from Iosegun; one, three from Charron; one, two from Rattlesnake [1977]; four, five, six and two, three from Fleeinghorse; and one, three from Dusty Lakes), whereas there were none in the previous example (again excepting complete lake units).

Multiple discriminant function analysis shows four discriminating variables. In order they are: Dio. inflata, Oligorchis n.sp., Dic. coronula, and R. cyrtoides. A Kruskal-Wallis test of mean abundances (Appendix 4) between these clusters shows less variation than in the 59 variable dataset. Still, however, there are significant variations in most of the frequent and abundant species.

Finally, cluster analysis was run on a reduced dataset that included only the 10 species comprising the recurrent group. Note that I have included Tuvensis A in the group since its contribution to similarity in samples is independent of its maturity. The results of this analysis are shown in Figure 7. Again at a coefficient of zero, four clusters are defined. Three clusters each contain one

Figure 7. Cluster analysis comparing individual birds with respect to the presence and abundance of the 10 helminth species comprising the recurrent group. The vertical axis represents the correlation coefficient. Numbers 1 through 4 on the stem lines delineate the four clusters produced at a similarity of 50%. See text for further discussion.



complete lake unit: Iosegun, Bistcho, and Murray Lakes. There are, however, no closest associations between pairs from the same lake. In fact, there are seven samples that cluster out at remarkably high similarity (≥ 0.8). These include samples two from Dusty, Chip, and Bellshill Lakes; sample one and five from Bellshill and Fleeinghorse Lakes respectively; and sample two from Charron and Lanes Lakes. It is interesting to note that on a reduced dataset, with ever-increasing similarity coefficients, not only do samples from the same lake show little similarity to each other, there are exceptionally high similarities between some samples from different lakes.

Multiple discriminant function analysis reveals only two discriminating variables (H. pusilla and Tuensis A) significant at $p < 0.05$. A comparison of variation in mean abundances between clusters for this reduced dataset (Appendix 5) shows that only D. coronula has no significant variation between clusters.

Discussion

Cluster analysis has been successfully applied in the past for classifying sites by the presence and abundance of species (e.g., Stephenson et al. 1970, 1972). The parallels between using cluster analysis in free-living assemblages and its use in the current analysis are not difficult to draw. Each bird was a sample and samples were clustered by the relative abundance of helminth species.

Results of cluster analysis do not support the

hypothesis that samples from the same lake can be treated as a unit. There was no strong tendency for all of the samples from a lake to fall in the same cluster groups (which were defined at 50% similarity). Neither was there a strong tendency for any given sample to be more highly correlated with another sample from the same lake.

Conclusions drawn from these observations seem obvious and related. First, there is an overall high degree of similarity in the helminth fauna of lesser scaup. Evidence for this comes from the coefficients at which clusters are formed. Never are high, or even moderate, negative coefficients generated. In fact, remembering that the coefficients can range from -1 for complete dissimilarity to +1 for complete similarity, all samples are fused into one cluster at coefficients slightly less than zero (-0.069, -0.093, and -0.142 respectively for the 59, 29, and 10 variable datasets). This is exceptionally high similarity. Furthermore, clusters appear to be differentiated by two components: the relative abundances of the frequent and abundant species and the presence/absence of infrequent species. Second, there is little evidence for considering bird helminth faunas from the same lake as being more similar to each other than to bird helminth faunas from other lakes. Thus the rationale for using each bird's helminth fauna as an independent infracommunity is strengthened.

Principal-Components and Rotated Factor Analysis

Principal-component analysis (hereafter, PCA) is a multivariate approach used to define structure in a large dataset when no a priori predictions are available. By design, PCA reduces a large set of correlated variables to a smaller set of statistically independent components that partition the total variance. The first principal component is the group of transformed variables that account for the greatest amount of variance in the original set of variables. The second principal component is the combination of variables, uncorrelated with the first component, that accounts for the greatest proportion of the remaining variance. Although Pimental (1976) indicates that PCA assumes the data are from a multivariate normal distribution, Dudzinski et al. (1975) have shown that this assumption need not be met.

One of the problems with PCA is the lack of criteria for determining when a sufficient amount of variance is explained by the successive components (Morrison, 1967). This problem can be alleviated by using factor analysis coupled with factor rotation. Whereas PCA attempts to determine the minimum number of independent variables necessary to account for most of the variance in the original dataset, factor analysis analyzes the intercorrelations within a set of variables (Cooley and Lohnes, 1971). Factor analysis is now frequently used as an intermediate step to generate factor loadings for subsequent

rotation (Seal, 1964). Rotation of factors is an attempt to determine simple structure and thus facilitate interpretations. Simple structure means that factors contain many large and many zero loadings, with few intermediates (Morrison, 1967).

Principal-component analysis is traditionally a technique used by taxonomists. Recently however, this potentially powerful approach to multivariate analysis has been applied to problems in community ecology. Holmes et al. (1979) used PCA to examine guild structure in 22 bird species. They found that the first three principal components collectively accounted for about 70% of the total variance. Futuyma and Gould (1979) examined insect-plant relationships and found that nine factors were needed to explain 75% of the total variance suggesting that the variations in the faunal composition are large in number.

The use of rotated factor analysis is rare in ecological work but was successfully applied to community analysis by Holmes et al. (1979) in the study mentioned earlier. The results of their rotated factor analysis confirmed their observations based on PCA.

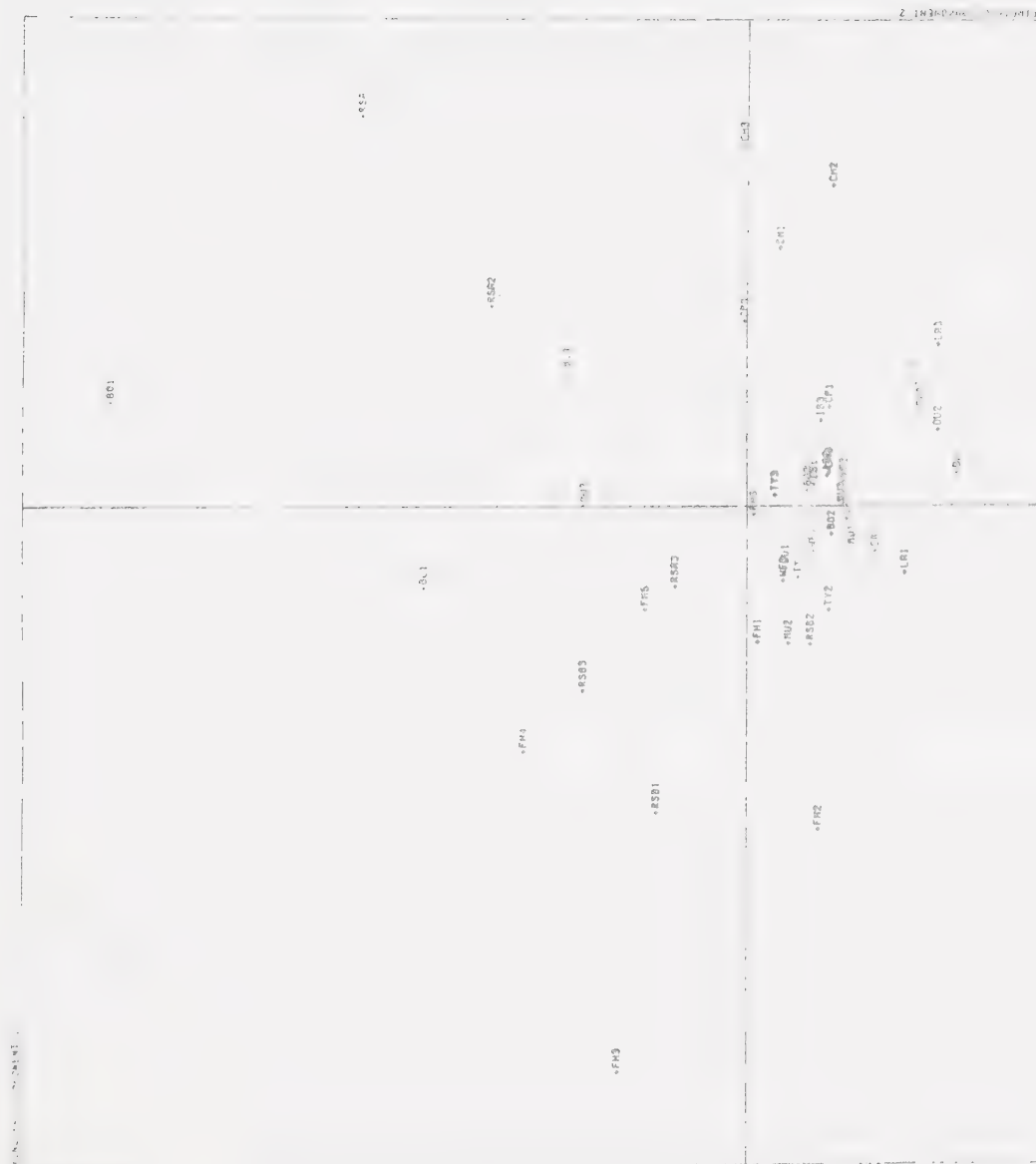
Principal-Component and Rotated Factor Analysis of Helminths in Lesser Scaup

Principal-component and rotated factor analyses were used to examine the relationships of the variables within

the dataset. Analyses already discussed strongly suggest that there is a characteristic group of helminths which account for a great deal of similarity between the birds. The use of PCA allows an examination of the samples with respect to uncorrelated components and can be used to further assess similarity. An intermediary principle-axis factorization provides factor loadings to be rotated using a Varimax rotation (discussed in Aspey and Blankenship, 1977). The resulting factor loadings depict the simple structure and can be used to further examine relationships between the variables. As noted earlier, there is no criteria for determining a desirable level of variance to be accounted for when using PCA. The levels most frequently used are 70 to 75% however, Morrison (1967) argues that extracting vectors beyond four or five components is usually fruitless and uninterpretable. For that reason, I have extracted, at most, the first four components in the following analyses. Based on earlier analyses, variables (helminth species) occurring in less than five samples were not important in determining either similarity or relationships within the dataset and they are excluded from further analysis.

Applied to all variables occurring in more than five samples, extraction of four components collectively accounts for only 47% of the variance. Ten components are necessary to account for 75% of the variance. The relationships between the 45 samples with respect to the first two components (30% of the variance) are shown in Figure 8. Note

Figure 8. Plot of the first and second principal component scores for the 29 variable correlation matrix. This includes all helminths occurring in more than five samples. Each point represents an individual sample (bird). See text for further discussion.



that with 30% of the variance accounted for, the pattern differs somewhat from that obtained using cluster analysis. The three samples from Charron Lake are reasonably close together as are the samples from Chip and Iosegun Lakes (the overstruck samples are samples two and three from Iosegun and Cowoki, respectively and three and one from Wolf and Dusty, respectively). In general however, replicate samples are scattered between the four possible quadrats and although not drawn on Figure 8, visual inspection of the factor scores for the third component (Appendix 6) suggest that these three sets of replicates would be separated (at a level of only 39% of the variance). Component one, accounting for 17% of the variance, appears to be related to the most frequent and abundant species while component two (13% of the variance) includes infrequent species with few individuals (compare eigenvectors from Appendix 6 with mean abundances from Table 5).

The relationships among the variables should be more interpretable following a principal-axis factorization and subsequent Varimax rotation. Table 8 presents the variables sharing at least 25% of the variance with a factor (based on all variables occurring in more than five samples). The amount of variance a variable shares with a factor is the square of the factor loading for that variable (Comrey, 1973). Thus, to share 25% of the variance, a factor loading of 0.5 is necessary and to share 50% of the variance requires a factor loading of 0.71. Because of the overall

Table 8. Varimax rotated factor analysis. Only variables sharing at least 25% of the variance with a factor are shown. Based on variables occurring in at least five samples. See text for further discussion.

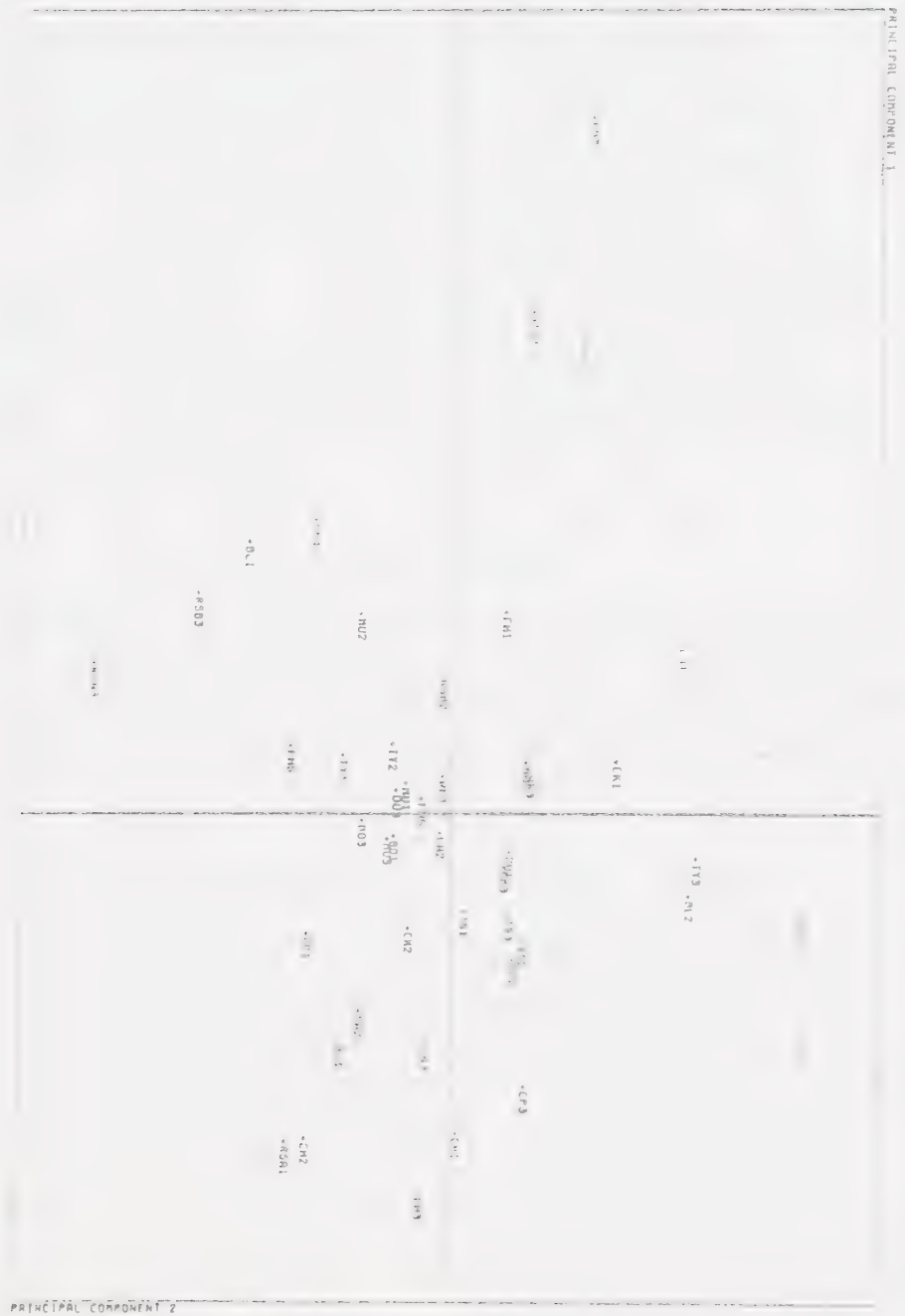
	FACTOR			
	1	2	3	4
Eigenroots	4.68	3.50	2.70	2.40
Percent Variance	15.8	12.3	9.3	8.1
Cumulative Variance	15.8	28.0	37.3	45.5
<u>Fimbriaria fasciolaris</u>	.532			
<u>Hymenolepis spinocirrosa</u>	.893			
<u>H. abortiva</u>	.754			
<u>H. pusilla</u>	.834			
<u>H. tuvensis</u>			.699	
<u>Tuvensis A</u>	.674			
<u>Lateriporus skrjabini</u>			.563	
<u>Retinometra pittalugai</u>				-.866
<u>Polymorphus marilis</u>	.501			
<u>Unciunia n. sp.</u>		-.688		
<u>H. microskrjabini</u>			.613	
<u>Corynosoma constrictum</u>	.522			-.580
<u>Diorchis n. sp.</u>				-.784
<u>Hymenolepis sp. 1</u>		-.888		
<u>Hymenolepis sp. 2</u>		-.693		
"O"		-.620		
<u>H. melanittae</u>	.603			
<u>Diorchis inflata</u>	-.714			

low variance accounted for by the factors, only variables sharing at least 50% of the variance with each factor are considered important. These factor loadings are underlined in Table 8. Factor one accounts for 16% of the variance. The important variables in this factor are the highly intercorrelated three species subgroup using H. azteca as an intermediate host. Factor two (12% of the variance) contains the infrequent species with the fewest individuals. None of the life cycles for these species are known. Factor three (9% of the variance) includes no species sharing even 50% of the variance with that factor. The highest values are for those species that use G. lacustris as an intermediate host. Factor four (8% of the variance) is not interpretable. It contains two species with high negative loadings one of which occurs frequently with moderate numbers of individuals (R. pittalugai), the other is infrequent with moderate numbers of individuals (Diorchis n. sp.).

Applied to the 10 variables in the recurrent group, PCA was much more informative. Only three components were extracted and these three components collectively account for 64% of the total variance. Viewed in two-dimensional space (52% of the variance), the 45 samples show good separation albeit with some tendency for the majority of samples to be near the origin (Figure 9). Samples from Iosegun Lake are relatively close in two dimension but would separate along the third component (Appendix 7).

Because of the relatively high proportion of variance

Figure 9. Plot of the first and second principal component scores for the 10 variable correlation matrix. This includes all helminths in the recurrent group. Each point represents an individual sample (bird). See text for further discussion.



accounted for by the first three components, zero loadings were reduced to those variables sharing 25% (factor loading of 0.5) of the variance with a factor (Table 9). The first factor (31% of the variance) includes species that were both very frequent and abundant. All four are species that use H. azteca as an intermediate host. The second factor (18% of the variance) includes frequent species with moderate numbers of individuals. Two of these species (H. downsi and P. marilis) require G. lacustris as an intermediate host; the third species can use Gammarus. The third factor (13% of the variance) includes frequent species with few individuals.

Discussion

The results of PCA were not as enlightening as previous analyses but do provide substantiating evidence to support the premise that samples from any particular lake are more likely to be similar to samples from a different lake than to replicate samples from the same lake. This is particularly obvious when the 45 samples are compared in terms of the first two components for the 29 variable dataset. With only 30% of the total variance accounted for, there is good separation of most replicates. Interpretation of the fact that 10 components are necessary to account for 75% of the variance seems obvious, the variance in faunal composition of the 45 samples cannot be explained by a few uncorrelated variables. Rather, the variance suggests that most of the helminth species exhibit independent

Table 9. Varimax rotated factor analysis. Only variables sharing at least 25% of the variance with a factor are shown. Based on variables in the recurrent group. See text for further discussion.

	FACTOR			
	1	2	3	4
Eigenroots	3.1	1.8	1.2	0.97
Percent Variance	70.3	18.1	13.0	9.1
Cumulative Variance	70.3	49.4	62.4	73.5
<u>Fimbriaria sociolaris</u>		.741		
<u>Hymenolepis spinocirrosa</u>	.681			
<u>H. abortiva</u>	.819			
<u>H. pusilla</u>	.874			
<u>H. tuvensis</u>		.878		
<u>Tuvensis A</u>	.698			
<u>Apatemon gracilis</u>			.823	
<u>Retinometra pittalugai</u>				.959
<u>Polymorphus marilis</u>		.666		
<u>Dicranotaenia coronula</u>			.721	

distributional patterns amongst the samples. This is emphasized when PCA is applied to the 10 recurrent group species. Examining the 45 samples in two dimension with respect to only those species which are a common part of each other's environment, there is still good separation of the samples but 52% of the variance is explained.

Varimax rotation of factors was not as useful as was hoped either, particularly when applied to the 29 variable dataset. However, the first factor does have exceptionally high loadings (sharing at least 50% of the variance with that factor) for the highly intercorrelated three species group determined earlier. In fact, when all variables sharing at least 25% of the variance are included, all but three (*Tuvenis* A, *P. marilis*, *H. melanittae*) are known to go through *H. azteca*. *Tuvenis* A has an unknown life cycle however, cysticercoids are identified primarily on hook length and structure, and *Tuvenis* A hooks and *H. tuvenis* hooks are virtually identical. *Hymenolepis tuvenis* cysticercoids have been reported regularly in both species of amphipods in Alberta (unpublished records, University of Alberta). Thus, *Tuvenis* A may well be using either or both of these intermediate hosts and was simply not recognized. More circumstantial evidence that *Tuvenis* A uses one of these intermediates is the simple fact that *H. tuvenis* has been reported from both. Other very closely related hymenolepidids (e.g., *H. spinocirrosa*, *H. pusilla*) use only one of the hosts suggesting host specificity at the

intermediate level. Polymorphus marilis uses G. lacustris as an intermediate host however, this is the one species for which there is prima facie evidence for facilitated transfer (Bethel, 1972). The life cycle of H. melanittae is unknown. This evidence suggests that the variables in the first and third factor are those species which cycle through the preferred food of lesser scaup.

Applied to the 10 recurrent group species, Varimax rotation was even more suggestive. The first factor has even higher loadings for the three highly intercorrelated species group, and includes these three species plus T. venis. A. This first factor is obviously related to species that use H. azteca as an intermediate host. The second factor has high loadings for three species all of which use G. lacustris as an intermediate host.

Faunal Similarity - Concluding Discussion

While I might be reproached for belaboring the issues in the previous analyses, I submit to the advice of Aspey and Blankenship (1977) "...a diversity of approach is desirable to produce the most complete understanding of a system's dynamics". Total understanding of the current system will be impossible without a substantial increase in our knowledge of the complete life cycles of many of the species and their required definitive hosts.

Even without this knowledge, some conclusions can be

drawn and some interesting ideas generated. Reiterating that replicate samples of lesser scaup are probably the closest thing to exact replicates available in a field study, there is a high degree of similarity, between infracommunities, of samples over a substantial portion of their breeding range. Perhaps the most interesting feature however, is that replicates from the same lake are generally less similar to each other than to samples from vastly different lakes. This has some interesting ecological implications. First, the samples (lesser scaup) themselves seem to be the most important variable to the helminths responsible for the similarity of those samples. This is apparent even when 55 other variables are examined. Second, helminth species which do not contribute to the basic similarity of the samples, over the entire set of samples, do not appear to provide any similarity within particular lakes either. In other words, they appear to represent chance occurrences. One might then suggest that the helminth infracommunities in lesser scaup are characterized by two elements: deterministic species that integrate these infracommunities, providing high similarity between samples, and the stochastic species providing most of the variance between samples. A further suggestion is that the deterministic component is composed primarily of two "intermediate host suites" of helminths: those cycling through H. azteca and those through G. lacustris. Unfortunately, the life cycles for the infrequent stochastic elements are unknown locally. If one can assume

that the life cycles of these are generally comparable to others in their respective genera, they typically cycle through copepods and/or ostracods.

The relationships among the variables also provide some interesting implications. The consistent relationships between *G. spinulosus*, *G. aculeatus*, and *G. pusillus* on the one hand and *H. tuvensis* and *P. marilis* on the other, are intriguing. They appear to be the helminth species that "belong" to lesser scaup. As such, they might truly be a more realistic recurrent group than the nine species previously suggested. Furthermore, their tight relationship may suggest long evolutionary association with not only the hosts, but with each other as well. They might be thought of as two co-accomodated (sensu Brooks, 1979) groups, one using *H. azteca* and the other using *G. lacustris* as intermediate hosts, but both using lesser scaup as definitive hosts.

The widespread generalists (e.g., *A. gracilis*) are difficult to define. They fit the classical description of habitat generalists, common in occurrence but never abundant, at least when compared to other species. Also, they tend to be species that are longer-lived, requiring substantially more time to complete their life cycles. They might well represent species with even longer evolutionary histories such that they have successfully exploited a number of different habitats, whereas the previous species seem to have exploited only lesser scaup. Butterworth (pers. comm.) has evidence to suggest that some of these "lesser

scaup" species (e.g., H. spinocirrosa, H. tuvensis) may invade other hosts although not nearly as consistently nor with the numbers seen in lesser scaup. Perhaps these species are currently in the process of exploiting new habitats. If this scenario is correct, one might well expect that there would be species that are currently invading lesser scaup while maintaining the bulk of their population in another (or other) host(s). This appears to be the case for at least two species, Retinometra cyrtoides, which is a parasite of ruddy ducks (Oxyura jamaicensis) and H. melanittae, a parasite of white-winged scoters (Melanitta fusca). Although there may well be other examples of this, further speculation is thwarted by lack of knowledge about life cycles for most of the species.

VII. Infracommunity Structure

I have presented evidence to suggest that there is a fundamental similarity amongst all samples of lesser scaup, that similarity of samples within lakes tends to be less than the similarity of samples between lakes, and that this similarity is due to a relatively small group of species. These interpretations are based solely on the presence and abundance of species and, although they are appropriate to addressing similarity questions, they only suggest broad structural features (i.e., distributions across samples). They do however, totally ignore any organizational relationships within the actual samples. It is at this latter infracommunity level that one might appropriately make further use of the data.

In an important theoretical contribution on community structure, Caswell (1976) suggests that functional and structural approaches to a system are not totally independent. He infers that one approach may be used in an attempt to provide information about the other or, more commonly, to elucidate the relationships between components within that particular approach. He notes that a functional approach addresses dynamics of behavior and development whereas a structural approach emphasizes the actual components.

In defining a structural approach, Caswell identifies five features of the components that merit attention: their nature, number, distribution, arrangement, and pattern of

interaction. If "their nature" refers to their basic biology (e.g., life cycles), then the former two features have been used in earlier arguments. It is the latter three features that will be addressed in the remainder of this thesis.

There are several important assumptions implicit in the following analyses that must be addressed. First, it should be noted that much of what I discuss will be features that most ecologists would liken to niche dimensions. Quite frankly, I have no idea what constitutes a "niche" for any of the helminth species. Classically, niche is most commonly related to food, space utilization, or a combination of both (see review in DeBach, 1966). I do not know the food requirements for any of the species involved in this study. Neither do I know, other than in a general sense, the availability or type of food along the continuum. Furthermore, the only data I have on space utilization is the linear distribution along a well-integrated continuum. I have no evidence for possible radial distributions, which have been considered important in some studies involving the discriminate, engulfing guild (e.g., Schad, 1963). The first assumption I make is that, although I cannot define a niche for these species, they define their own realized niche by their distribution. The rationale suggested here is that, when averaged across all 45 infracommunities, these average values, and their variances, provide the best available measure of realized niche. The second assumption I make is that these same distributions, when summed across all 45

infracommunities, provide the best available measure of a species' fundamental niche. In other words, it is a clue to their potential distributions. The true fundamental niche cannot be determined without experimentation. I also assume that the median individual of a population in each sample is the best available measure of its location in that sample and that for each species, the mean across samples, of the median within samples, represents the best measure of the preferred location of that species. Finally, I assume that some resource(s) are (or become) limiting within the gut. This has not been addressed for the present system, but experimental evidence has demonstrated that nutrients, particularly carbohydrates, can be limiting (Read and Rothman, 1958; Read, 1959; 1970). We do not know to what extent, if any, nutrient availability or concentrations vary in natural systems.

Linear Distributions of Scaup Helminths

One of the striking features of this system is the limited, sequential distribution of helminth species along the intestinal continuum. Averaged across 45 samples, the measures of distribution (median point, range, and end points) show not only an apparent fidelity by species to particular portions of the continuum, but also a sufficient amount of variability to produce somewhat different patterns under different conditions. Average values and variances for

the distributional measures of each species were presented in Table 5. In this section, I examine these distributional measures and the patterns that emerge.

For most species, variances of the median points were small (Table 5) suggesting considerable predictability in the location of each species. Considering that the entire continuum might be available to each species, the variance of those median points are quite small: 16%, or less, of the continuum. With three exceptions, the variance of each species' median point was between 10 and 20% of the species' maximum range. The exceptions, H. melanitiae, Hymenolepis sp. 1, and "O", are infrequent species with small ranges and relatively large variances.

The sequence of species' distributions along the continuum was highly predictable. A series of 50 random pairings, drawn from the complete dataset, produced very high rank correlations (ρ : mean=0.89, s.d.=0.07, range=0.63-0.99). The number of species in common for these random pairings ranged from 5 to 16 (11 ± 2).

With only one exception, the median point of each species' population within a sample was not correlated with the number of individuals of that species in the sample, suggesting that the median point is typically independent of population size. The exception may be an important one: Hymenolepis spinocirrosa, has a median point that is significantly ($p < .001$) negatively correlated with the total number of H. spinocirrosa in each sample. As the population

level of this species increases, the median point moves anteriorly along the gut.

The average range occupied by individual species spanned a third or less of the continuum. One species, H. spinocirrosa, occupied a substantially greater portion (41%). For most species, including all of the more frequent species, the range in each sample was highly correlated with the total number of individuals of that species (see Table 10). The only moderately frequent species whose range was independent of total numbers was D. coronula.

The end points of distributions show several interesting features. First, there is no portion of the continuum that is not habitable by at least four helminth species. Second, considering average end points and their respective variances, there is good reason to suspect considerable overlapping between sequential species pairs along the continuum. Finally, correlations, within samples, between the total number of individuals in a species and the end points of that species' distribution show four patterns. The first pattern that emerges is that for the less-frequent species: neither the anterior nor the posterior end points are correlated with the number of individuals. The remaining patterns are illustrated by species in which there are significant correlations between total number of individuals and end points of distribution (Table 10). The second pattern is that in which there is an equilateral spreading about the median. As the population of the species

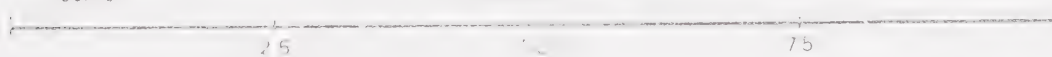
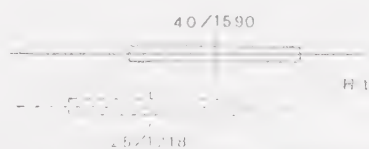
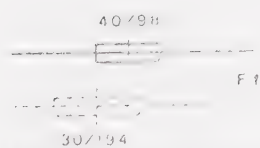
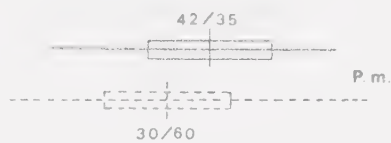
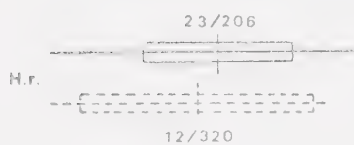
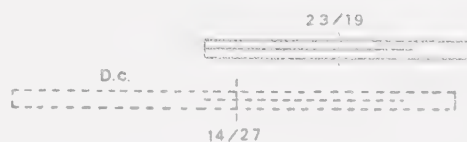
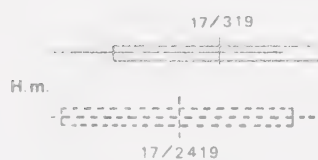
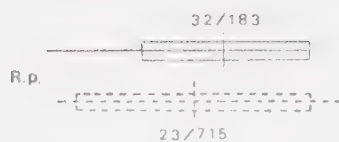
Table 10. Direction of significant correlations between the total number of individuals in a species and that species' anterior or posterior end points. Also included are those species whose range was significantly correlated with the total population of that species. All data represent correlations within samples and only species with significant correlations shown.

	Anterior End Point	Posterior End Point	Range
<u>Fimbriaria fasciolaris</u>	-	+	+
<u>Hymenolepis spinocirrosa</u>	-	0	+
<u>H. abortiva</u>	-	+	+
<u>H. pusilla</u>	-	+	+
<u>H. tuvensis</u>	-	+	+
<u>Tuvensis A</u>	-	0	+
<u>Echinoparyphium recurvatum</u>	0	+	+
<u>Apatemon gracilis</u>	-	0	+
<u>Lateriporus skrjabini</u>	-	+	+
<u>Retinometra pittalugai</u>	-	+	+
<u>Polymorphus marilis</u>	-	+	+
<u>Dicranotaenia coronula</u>	0	+	0
<u>Unciunia n. sp.</u>	0	+	+
<u>H. recurvata</u>	-	0	+
<u>H. microskrjabini</u>	-	0	+
<u>Diorchis excentricus</u>	0	+	+
<u>Cotylurus hebraicus</u>	0	0	+
<u>Corynosoma constrictum</u>	0	0	+
<u>Capillaria obsignata</u>	0	0	+
<u>R. cyrtoides</u>	0	0	+

increases, the anterior end point moves anteriorly and the posterior end point moves posteriorly. These species include E. fasciolaris, H. abortiva, H. pusilla, H. tuvensis, L. skrjabini, R. pittalugai, and P. marilis. The third and fourth patterns are those in which there is unilateral movement of end points. Five species show a pattern in which the anterior end point moves anteriorly in response to increased population levels while the posterior end point does not move significantly. The species showing this anteriopad movement are: H. spinocirrosa, H. recurvata, H. microskrjabini, tuvensis A. and A. gracilis. The remaining four species (E. recurvatum, Dio. coronula, Unciunia sp. and Dio. excentricus) show the opposite unilateral movement. As population levels of these species increase, the posterior end points move posteriorly while the anterior end points show no significant movement.

In general, the variances associated with these derived, distributional features of median points, end points, and ranges are low, suggesting that the helminth species are not distributed in a haphazard fashion. There is a further method by which the predictability and constancy of these data might be examined. Hair (1975) used the same methods to study the distribution of helminth species along the intestine of 30 adult lesser scaup collected from Cooking or Hastings Lakes, Alberta. Figure 10 presents derived data on the medians, end points, ranges, and numbers of individuals for the common helminth species found in both

Figure 10. Comparison between Hair's (1975) results on linear distributions for the 11 most abundant species in his analysis and the distributions of the same species in the current analysis. Data presented are derived medians (vertical bar) and 1 standard deviation (box). The length of the line represents the average range occupied. Hair's data are in dashed lines, the present data in solid lines. Values associated with each distribution are the number of samples infected/mean number of individuals found. Horizontal axis represents an intestinal continuum. F.f.=Fimbriaria fasciolaris, L.s.=Lateriporus skrjabini, H.r.=Hymenolepis recurvata, H.m.=Hymenolepis microskrjabini, H.s.=Hymenolepis spinocirrosa, R.p.=Retinometra pittalugai, H.t.=Hymenolepis tuvensis, H.a.=Hymenolepis abortiva, P.m.=Polymorphus marilis, D.c.=Dicranotaenia coronula, H.p.=Hymenolepis pusilla.



Hair's study (dotted lines) and the present study (solid lines). There is remarkably good correspondence between the distributions of individual species along the continuum. Perhaps the greatest differences are for L. skriabini and Dic. coronula. In the present study, L. skriabini had the bulk of its populations posterior to H. recurvata as opposed to anterior as in Hair's data. The anterior end point of Dic. coronula was substantially more posterior in the present study than in Hair's. In terms of average numbers, Hair found substantially more E. fasciolaris, R. pittalugai, and H. microskriabini and less H. pusilla than in the present study. In a third study, Hair and Holmes (1975) examined the distribution of helminth species along the continuum of 10 lesser scaup collected from Cooking or Hastings Lakes, using slightly different techniques. They cut the intestine into 10cm sections rather than the 5% sections in the other studies. Thus the number of sections was a function of the length of the intestine and similarly numbered sections were not directly comparable between samples. Generally, however, their data agree with the observations of the two studies noted above.

As a final note, these analyses were performed using the total number of individuals in a population. These same analyses were also performed using only the mature or only the immature individuals. Except for the obvious (i.e., Tuvenis A which never matured), there were no significant differences in the observations using the different

datasets.

Discussion

The results of these measures of linear distribution seem rather conclusive: the abundant and frequent helminth species in these infracommunities occupy predictable locations along the resource gradient. This observation is consistent with that of Hair (1975) and Hair and Holmes (1975).

The very low variances associated with the median point would suggest that it is a useful predictor of location. Although most species' ranges were correlated with population size, the medians, with one exception, show no significant correlations with population size. This further enhances the usefulness of the median and suggests that the median point represents the prime location along the gut. The exception is *H. spinocirrosa* which appears to have a broader prime location than other species.

Other distributional measures show interesting, and suggestive, relationships with population size. The lack of any apparent relationship between distributional measures and population size in the infrequent species may be due to one or more of three factors. First, because of the low number of samples infected, it may simply be an artifact of the dataset. Second, it may be that their populations are relatively small and constant (but see the variances in Table 5). Finally, they may simply represent stochastic elements, unaffected by population size. Although the second

explanation seems unlikely, either the first, the third, or a combination of the two may be operational.

An additional four species (Cot. hebraicus, Cor. constrictum, Cap. obsignata, and R. cyrtoides) are frequent but never abundant. Neither the anterior nor posterior points of these four species are correlated with respective population size but their ranges are. Thus, as their population levels increase, their range expands but in an unpredictable fashion.

Seven other species show a similar pattern of increased range with increased population size, but in a predictable equilateral fashion. In short, they show unimpeded range extension.

All of the remaining species show unilateral expansion from the median. Hymenolepis spinocirrosa, H. recurvata, H. microskrjabini, Tuensis A, and A. gracilis all exhibit an anterior range extension in response to increased population levels. With the exception of Tuensis A, these species are all found in the anterior region of the intestine.

Dicranotaenia coronula, Dio. excentricus, Unciunia n. sp., and E. recurvatum show the opposite response: a significant posteriad extension. Dicranotaenia coronula and Dio. excentricus are species found in the posterior portion of the intestine. The remaining two species are found in the anterior portion, frequently in the first section, thus an anterior movement would be impossible. These latter observations suggest that some helminth species in these

infracommunities are unable to expand freely along certain portions of the continuum. Whether this is due to interactions with other species or to physiological conditions prevailing in the (apparently) unoccupiable portions remains a question to be addressed experimentally.

In summary, measures of location suggest that the species have discrete regions of preference, but, in most cases, they may exhibit predictable changes in response to changing population levels. Perhaps more interesting, the sequence of species along the intestine is highly predictable.

Community Models

The patterns discussed in earlier sections imply a definite element of structure within these intestinal infracommunities, particularly, the predictable sequence of distributions.

There is a growing body of literature in which biologists are developing conceptual models in an attempt to understand patterns observed in nature. Caswell (1976) presents a recent review of these models as they apply to questions of community structure.

In a recent reinterpretation of MacArthur's celebrated "broken-stick" model, De Vita (1979) provides theoretical and empirical arguments to suggest that the model may be used to examine niche distances along a single continuum. In

his reinterpretation, random points are thrown on a stick of length c (which represents the length of a continuum). The points represent the means of resource utilization functions along the continuum, and the lengths of segments between adjacent points represent niche distance between adjacent species. Differing from the original interpretation, each point, rather than each segment, represents a species.

De Vita (1979) notes "...in the present model, assumptions relating to variance of utilization are not taken into account and thus do not play any role in determining the species' position along the continuum as in other theoretical models....In this way, the model...does not necessitate assumptions concerning niche overlap" The model has one assumption: that in using a resource, species do not interact sufficiently to affect partitioning of the resource. The model requires that a single resource dimension be considered. In short, it is a random model, assuming non-interaction along a single environmental axis.

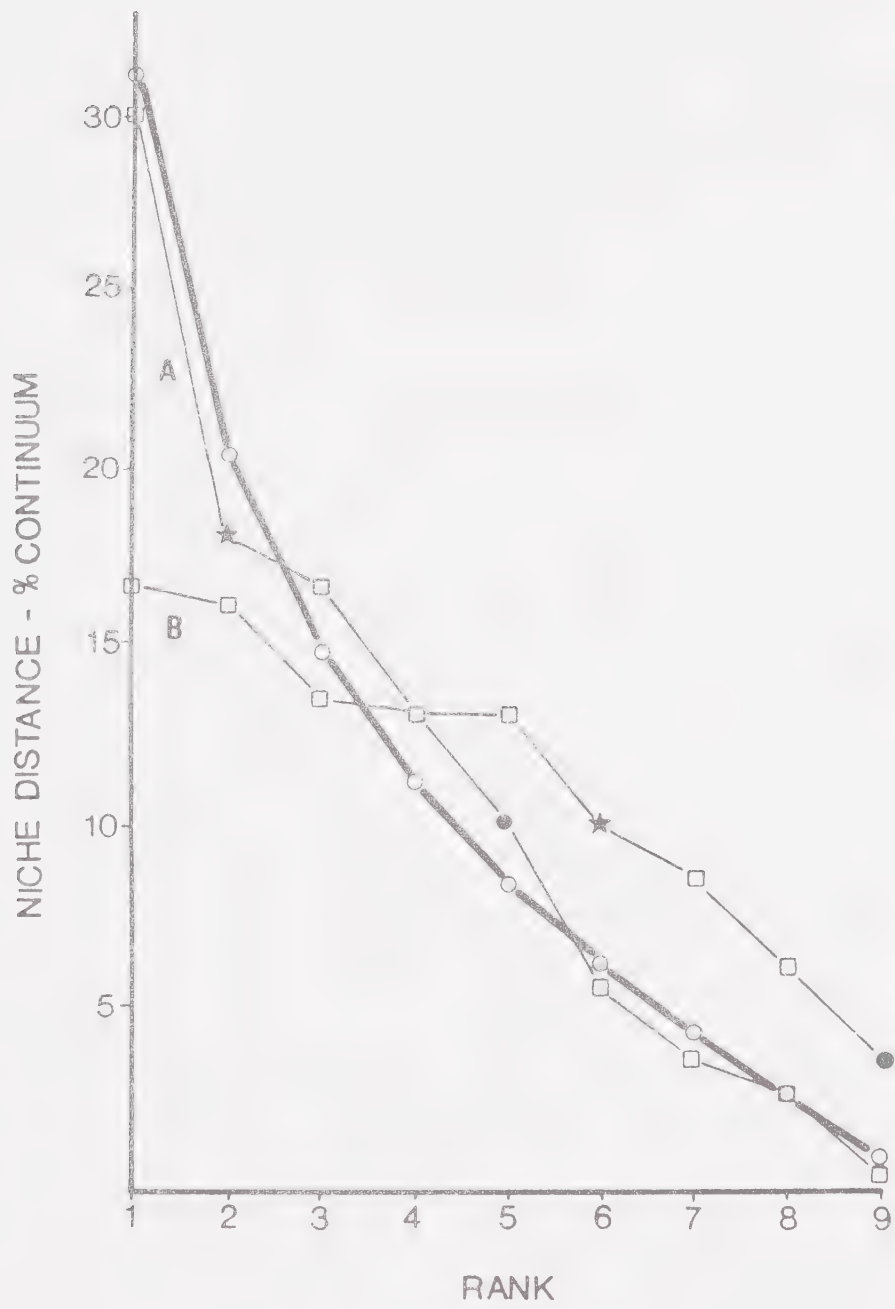
There are two reasons why this would appear to be a particularly appropriate model with which to compare helminth species along the intestine for random distributions. A single resource axis is appropriate to helminths, since location along the gut is correlated with most environmental factors (see previous discussion). Second, the resource gradient is finite, so that the endpoints of the continuum are objective, not subjective, as in the three datasets used by De Vita to test the model.

Intestinal Helminth Parasites and the Broken-Stick Model

The model was used to generate predicted values for niche distances in systems with $n=5-20$ species and a resource axis 100 units long. The mean and standard deviation was then calculated for each n . Observed values were calculated as follows: For each infracommunity, the median of each species' population was expressed as a percentage distance along the small intestine and the distance between adjacent pairs calculated. These distances were then ranked and the mean and standard deviation calculated. These values were then tested against observed values using the sign test. The significance of the sign test was determined using values of t as suggested by Sokal and Rohlf (1969).

Initially, the distributions of all helminth species with population levels greater than 10 individuals were compared with random distributions generated by the broken-stick model. There were no six species or nine species infracommunities; otherwise, the number of species per infracommunity ranged from a low of five to a maximum of 20. Figure 11 is representative of the distribution of niche distances for the two samples of 8-species infracommunities versus the predicted distributions of an 8-species infracommunity. The mean distances in these infracommunities could not be distinguished from the predicted mean distances. From Figure 11 it can be seen that the standard deviations of the mean distances for RSB2 are very close to

Figure 11. Niche distances, ranked by size, of intestinal helminths in two infracommunities. Open circles represent predicted distances generated by the broken-stick model; open squares represent empirical distances; stars represent the upper limits to the continuum, solid circles the lower limits. RSB-2=A, Ty-2=B.



predicted values whereas the standard deviations for TY2 are substantially different.

None of the mean distances in any of the 45 infracomunities could be distinguished from predicted means, however, almost all of the standard deviations for these means showed the pattern typified by TY2 (Figure 12). The mean deviation for the observed distributions was significantly less ($t=4.32$, $p<.05$) than predicted from the model. Because most infracomunities exhibited the pattern of standard deviations shown by TY2, an additional test was performed. Five niche distances (the maximum, second largest, median, second smallest, and the minimum) were compared against the respective predicted distances from the model, using a sign test (Table 11). Note that the maximum and second largest distances were significantly smaller while the median and second smallest were significantly larger. There was no significant difference between observed and predicted minimum distances; both were close to zero.

A seemingly logical step was to reduce the dataset and compare the observed distributions of the species comprising the predominant absorber guild with the predictions of the model. This resulted in infracomunities ranging from five species to 18 species. Figures are not presented for these comparisons, they show essentially identical patterns to those seen in Figure 11. Again, the mean deviations were significantly less ($t=3.73$, $p<.05$) than predicted. In comparing the five niche distances, virtually the same

Figure 12. Standard deviations of the mean distances for each infracommunity. Solid line represents predicted standard deviation.

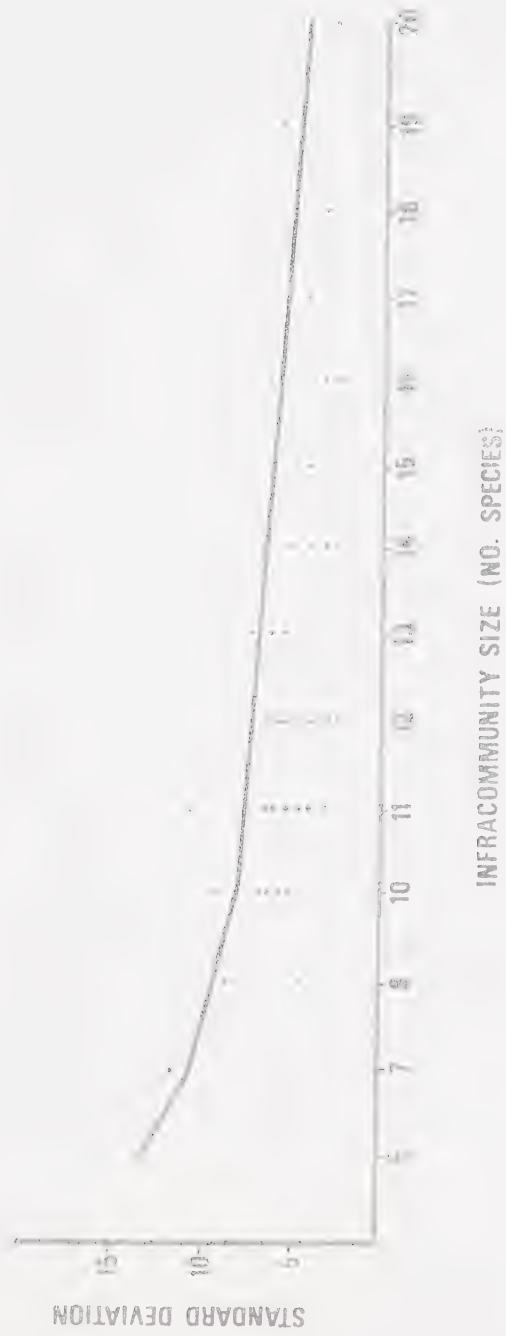


Table 11. Summary of the observed and predicted distances. Observed distances are the mean values for those obtained from the current dataset. Predicted values are those derived from De Vita's model. Inequalities reflect the observed distances difference from the predicted. Differences tested for significance ($p < 0.05$) with Sign Test.

	Distance			
	Maximum	Second	Middle	Second Minimum
All species	<	<	>	=
Absorbing guild	<	=	>	>
Species flock	<	<	>	=

pattern to that noted above was revealed: the larger distances were significantly less, the middle and smaller significantly greater, and the smallest not different.

Finally, the distributions of species in a large "species flock" (very close phylogenetic relationship) were compared with the model. This species flock accounts for almost all of the individuals in the system and includes H. spinocirrosa, H. recurvata, H. luensis, H. arcuata, H. abortiva, H. pusilla, and H. microsclabini. There were no two species infracomunities. Otherwise, infracomunity size ranged from one species to six species. As in the previous two analyses, the mean deviation was significantly less ($t=4.63$, $p<.05$) than predicted by the random model. A comparison of the five niche distances revealed a slightly different pattern for this reduced dataset than was seen in the previous analyses (Table 11). As in the others, the maximum distance was again significantly smaller than predicted, however, the second largest distance was not significantly different. In addition to the median and second smallest, the minimum distance was also significantly greater.

Returning to Figure 11, note that the ends of the continua (as shown by a star for upper limits and a solid circle for lower limits) do not necessarily fall at the largest intervals as suggested by De Vita: "The largest deviation between predicted and observed data for all three assemblages most often corresponds to the observed distances

at the furthestmost ends of the resource continuum; i.e., the distance between the resource minimum and the first species' mean and the distance between the resource maximum and the last species' mean.... These intervals can hardly be considered niche distances but are nevertheless necessary for model comparison, since equation (1) does not specify the order of generated segment lengths. Additionally, the tendency for the largest segments to fall at the ends of the continua suggests that these portions of the continua may be nonutilizable (i.e., nonproductive, unavailable, or of a harsh physical nature) and thus not appropriate to the present analysis."

In the current analysis, the ends of the continua are available and are used (though not to the same extent as the middle portion - see below). However, using medians as locators does mean that there is a reduced probability for the location to be very close to the ends. Therefore, a further test of distributions was appropriate.

The continuum was divided into ten equal sections, each section representing 10% of the continuum. The number of medians falling in section one (i.e., 0 to 10%) was counted, the number in section two (11 to 20%) was counted and so forth. If the distributions were either random or uniform, there should be an equal (or nearly so) number of medians in each of the ten sections. The observed versus the predicted results can then be tested using a Chi square analysis. The first and last sections were eliminated because of the

mathematical properties of the median (as noted above).

Thus, the analysis was based on eight sections.

When all of the species were considered, the distributions of the medians were not significantly different than predicted for an equal distribution between the eight sections (Chi square = 10.79 vs Chi square of 14.07 at $p < .05$ and 7 d.f.). The distribution of the medians (67,55,62,67,69,85,64,52 in sections 2 to 9, respectively) shows some tendency for the middle of the gut to be more preferred than the ends. When applied to the large absorber guild and to the species flock, the same analysis shows a different pattern. The distribution of medians for both of these datasets are significantly different than predicted (Chi square = 20.01 and 48.67, respectively versus 14.07 with 7 d.f.). The distribution of the medians in sections 2 to 9 was 46,39,47,59,60,77,58,50 and 8,16,26,30,42,38,9,18 respectively for the absorber guild and the species flock. For both the absorber guild and the species flock, the middle of the gut appears to be a more preferred location than either of the ends. By subtracting the data of the absorber guild from that of the entire dataset, the distribution of the non-absorbers can be determined. They show a very strong preference for the anterior portion of the gut (21,16,15,8,9,8,6,2) and their distributions are significantly different than predicted (Chi square = 25.67 vs Chi square of 14.07 at $p < .05$ and 7 d.f.).

Discussion

When compared with the expected values from a random model, the results are not compatible with a stochastic assemblage. The significantly lower variances of the observed data compared to the predicted variances strongly supports this conclusion. Furthermore, all three datasets show this same pattern of smaller variance, that the largest distances are smaller, and the smallest distances are larger, also suggests a pattern more regular than expected by chance. This regularity of pattern is apparent when the three datasets are compared with a model which apportions the medians in equal sections along the continuum. The lack of a significant difference between the observed and predicted values for the entire dataset is interesting, suggesting a pattern more regular than a random arrangement, but not uniform as was shown by the variances. The two components of the entire dataset, the absorber guild and the non-absorbers, are each significantly different than would be predicted by an equal apportioning of the medians suggesting a complementarity of distributions between the two groups.

The linear distributional data presented earlier suggested a predictability in the order of occurrence of species and in their general location along the continuum. The results presented here suggest that the locations of these species are not spread randomly along the intestine, but are distributed more regularly than expected by chance.

In short, the structure of these infracommunities is not that of stochastic, non-interactive assemblages. Rather, they show features one might expect for an integrated, deterministically assembled infracommunity. In the following section, analyses of interspecific associations will be examined in an attempt to explain these patterns.

Patterns of Interaction

At this point it would seem hard to deny that the helminths comprising the intestinal infracommunities in lesser scaup show not only regularity in distribution, but an apparent specificity to particular areas along the continua. Yet the data on end points of distribution (and their variances) presented earlier in Table 5 suggested that a considerable amount of overlap was possible among adjacent species. This raises an important question: What is the pattern of coexistence within infracommunities?

The search for patterns of coexistence has generated a plethora of indices purported to measure niche overlap and, by inference, competition (e.g., Colwell and Futuyma, 1971; Pielou, 1972). None has been found universally acceptable. In fact, it seems that no sooner is a new index proposed (e.g., Hurlburt, 1978), than it is criticized and a newer index is proposed (e.g., Petratis, 1979). The problem seems to arise from the interpretation of the results of any of these indices in light of the assumptions implied by the

index or those assumptions necessitated by the dataset.

Justification for the assumptions related to the present dataset have been presented earlier. However, one assumption requires further elaboration. Earlier I suggested that the distribution of a species, summed across all 45 infracommunities, provided the best available measure of that species' fundamental niche. For the following analyses, I have created an artificial "46th bird", in effect, the sum of all helminth species along each section of the intestine. All analyses performed on individual infracommunities were also performed on this "fundamental infracommunity". The rationale for using such an approach is that, considering the very abundant species, the average niche overlaps would approximate random draws from the parent (summed distribution) population. As such, statistical tests can be used to determine if the realized niche overlaps (average data) differ significantly from fundamental niche overlaps (summed data). A significant reduction from fundamental niche overlaps to realized niche overlaps is interpreted as evidence for interaction between species.

To measure niche overlap, I first use perhaps the simplest method of all, percent similarity (equation 1 in Hurlbert, 1978). This method measures the proportion of individuals in two populations having identical distributions. In short, it provides a measure of the minimum proportion of actual overlap between adjacent species. That is also how I interpret the results: the

minimum amount of overlap between adjacent species pairs along the continuum.

Another simple method for measuring niche overlap, but one that takes account of the respective species' niche breadths, is that of Levins (1968) (equation 13 in Hurlbert, 1978). Standardizing by niche breadths results in asymmetrical overlap and, in effect "measures how much a particular species' utilization curve...overlaps that of another species" (Petraitis, 1979).

Data on average symmetrical overlaps, their standard deviations, and the fundamental overlaps (46th bird) are presented in Appendices 8, 9, and 10, respectively. These same data for asymmetrical overlaps are presented in Appendices 11, 12, and 13, respectively.

Because of the ordered array of medians and specific locations of species discussed earlier, species at opposite ends of the continua exhibited no fundamental overlap. Inclusion of overlap data for species in which there was no fundamental overlap in any of the analyses would be meaningless, hence comparisons cover only species with some overlap between fundamental niches. Average symmetrical overlaps between species for which there was fundamental overlap ranged from less than 1% (essentially no realized niche overlap) to 100% (complete overlap). Average asymmetrical overlaps ranged from less than 1% to over 100% (see Levins, 1968 for interpretation of overlaps greater than 100%).

Between the 16 most frequent species, average overlaps ranged from less than 1% to 46% and from less than 1% to 65% for symmetric and asymmetric measures, respectively.

Within the intermediate host suites, symmetric and asymmetric overlaps ranged from less than 1% to 35% and from less than 1% to 54%, respectively, for the Hyaella suite. For the Gammarus suite, these same values ranged from less than 1% to 27% and from less than 1% to 41%. The average symmetric and asymmetric overlaps within the Hyaella suite were 10% and 12% respectively; the same average overlaps within the Gammarus suite were 10% and 13%.

When the overlaps between the species comprising each of the two suites were compared, the symmetric overlap ranged from less than 1% to 46%, the mean overlap between members of the two suites was 15%. The same comparisons for the asymmetric overlap ranged from less than 1% to 59% with a mean of 15%. There was no significant difference between overlaps when within suites were compared to between suites (Mann-Whitney U test).

Because the range of a species distribution was correlated with the number of individuals, the overlaps among the three most abundant species were compared in the infracommunity with the largest number of individuals (CH 2, $n=108,477$) and that with the smallest (FH 2, $n=81$). In the largest infracommunity, the symmetric overlaps between H. spinocirrosa ($n=42,767$) and H. abortiva ($n=17,190$) and between H. abortiva and H. pusilla ($n=27,910$) were less than

1% and 1%, respectively (to be compared with a fundamental overlap of 5% and 4%, respectively). For the smallest infracommunity, the symmetric overlaps between H. spinocirrosa (n=12) and H. abortiva (n=26) and between H. abortiva and H. pusilla (n=13) were 0 and 31%, respectively (to be compared as above). Values for asymmetric overlaps show identical patterns. Extending this analysis to the entire set of 45 infracommunities, there were no significant correlations ($p < .05$) between the abundance of H. spinocirrosa and H. abortiva and their overlaps ($r = 0.08$ and 0.3 , respectively) or between the abundances of H. abortiva and H. pusilla and their overlaps ($r = 0.2$ and 0.04 , respectively).

Figure 13 presents the results of significance tests (t-tests) comparing the average realized niche overlaps (symmetric) versus the fundamental niche overlaps for the 16 most frequent and abundant species. Note that almost all average realized niche overlaps are very highly significantly smaller than fundamental niche overlaps. Dicranotaenia coronula shows some tendency to have realized overlap not significantly different than fundamental overlap with some species in the anterior portion of the gut. Figure 14 presents similar results for asymmetric overlaps. Again, D. coronula shows the same pattern. Examination of individual infracommunities for the distribution of this species shows that very few individuals are found anterior to section 15 (where the non-significant overlaps occur).

Figure 13. Results of significance tests comparing symmetric niche overlaps for the 16 most frequent and abundant species. Comparisons were made between the realized overlaps and the fundamental overlaps (see text for elaboration). ***= $p < .001$, **= $p < .01$, *= $p > .05$, NS=not significant, 1=average overlap $< .001$, 2=No fundamental overlap.

Figure 14. Results of significance tests comparing asymmetric niche overlaps for the 16 most frequent and abundant species. Comparisons were made between the realized overlaps and the fundamental overlaps (see text for elaboration). Legend same as Figure 13.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. <u>Enallagma cyathigerum</u>	-	*	*	*	NS	NS	*	***	***	NS	*	2	2	2	1	2
2. <u>Enallagma cyathigerum</u>	***	-	***	***	***	***	***	***	***	***	*	*	*	*	***	*
3. <u>H. cyathigerum</u>	***	NS	-	***	*	NS	NS	***	NE	***	***	-	***	1	NS	***
4. <u>Apateon gracilis</u>	***	*	***	-	***	NS	NS	***	NS	*	*	NS	***	NS	*	***
5. <u>Lateriporus skryabini</u>	***	***	***	***	-	***	***	***	***	***	-	***	***	1	***	1
6. <u>H. Microskryabini</u>	NS	NS	***	***	*	-	NS	***	***	1	1	NS	1	2	NS	2
7. <u>Retiporella littoralis</u>	***	***	NS	***	***	*	-	***	***	***	***	NS	***	***	NS	***
8. <u>H. spirochaeta</u>	***	***	***	***	***	***	***	-	***	***	***	NS	***	***	NS	***
9. <u>H. turgida</u>	***	***	***	*	***	***	***	***	-	***	*	*	***	*	NS	***
10. <u>H. aboulayi</u>	NS	***	***	NS	***	***	***	***	***	-	*	***	***	***	*	***
11. <u>Cotylurus hebraicus</u>	2	1	***	***	***	1	***	***	***	***	-	***	*	NS	NS	***
12. <u>Polyporella hebraicus</u>	2	1	1	NC	***	NS	*	NS	*	***	***	-	*	*	***	***
13. <u>Tuvensis A</u>	2	*	***	NC	***	***	***	***	***	***	***	***	-	*	*	***
14. <u>Corynophora constricta</u>	2	1	1	NS	1	2	***	***	***	***	NS	***	***	-	***	***
15. <u>Dicranotaenia coronata</u>	1	1	NS	NS	***	NS	NS	NS	***	***	NS	***	***	***	-	***
16. <u>H. pallida</u>	2	2	***	***	1	2	***	NS	***	***	NS	*	NS	*	*	-

The majority of species that were moderately frequent (e.g., found in >5 infracommunities) but with few individuals, showed different patterns. For example, the symmetric overlap between R. cyrtoides and H. melanittae was 100%. The asymmetric overlap of R. cyrtoides on H. melanittae was 100%; the reciprocal overlap was also 100%. Neither the symmetric averaged realized niche overlap nor the asymmetric mean niche overlap differed significantly from the respective fundamental niche overlap. Fifty-eight percent of the realized niche overlaps for these moderately frequent species were not significantly different from fundamental overlaps. Only 17% of the realized niche overlaps for the infrequent species (e.g., found in <5 infracommunities) differed significantly from fundamental niche overlaps.

Discussion

Holmes and Price (1980) recently reviewed the question of how similar species can be in their niche exploitation patterns. Lacking empirical evidence for parasite systems, they accepted niche overlaps of 70% (basing this figure on arguments presented by Hutchinson, 1959; McClure and Price, 1976; Pianka et al., 1979) or less as a conservative estimate to distinguish species having different niche exploitation patterns.

Applying their estimate to the current dataset, the frequent and abundant species all exhibited different niche exploitation patterns along the continuum. The magnitude of

that difference was enhanced when species in either of the intermediate host suites were considered. When either the moderately frequent species with few individuals, or the infrequent species, were considered overlaps frequently exceeded 70%, often by a substantial amount.

Again considering the frequent and abundant species, their realized niche overlaps were generally significantly less than their fundamental niche overlaps whereas the remaining species generally showed no significant difference between realized and fundamental overlaps.

Collectively, these results suggest that the frequent and abundant species in these infracommunities represent deterministic elements, with little or no overlap among adjacent species. Conversely, the more infrequent, scarcer species show broad overlap, either with the deterministic elements, or among themselves, suggesting that they represent stochastic elements.

Restricted to the deterministic elements, these data lend support to Menge and Sutherlands' (1976) contention that competition will be, or was, the primary organizing force in trophically simple communities. These species all show significant reductions from fundamental to realized niches.

Infracommunity Structure - Concluding Discussion

Although various mechanisms invoked to explain

community structure have been discussed in the literature for a number of systems, this has not been done, to the same depth, for helminths. Because of this, a more thorough review of the pertinent hypotheses generated to explain structure in helminth communities will be presented.

Holmes (1973) reviewed a substantial amount of the available literature on the distributions of helminth populations in a variety of host species. He concluded that interspecific interactions between these helminth species were a major force in producing community structure. More specifically, he presents a review of the evidence to suggest that selective site segregation, as opposed to interactive site segregation, may be the primary mechanism resulting in the observed distributions.

Price (1980), examining much the same evidence as Holmes (1973), but also extending his review to include other forms of parasitism (e.g., parasitoids, viruses, etc.) argues a different hypothesis. He too views the structure in parasite communities as largely non-interactive as did Holmes. However, based on his interpretation of the available evidence, he suggests that most resources available to parasites are under-utilized and there are "vacant niches" (using the Hutchinsonian [Hutchinson, 1957] concept of the niche). Thus, species packing is low in most parasite communities, hence the probability of interspecific encounter is low, and the pressures for interaction are rare to non-existent. Specifically, Price puts forth the

hypothesis that parasite communities exhibit patterns consistent with chance colonization by specialists.

Wilson (1969) advanced the theory that there were four phases in the development of a community. The initial phase is one of "non-interactive species equilibrium" which is essentially what might be expected when resources are under-utilized. Colonization is rapid and populations do not reach sufficiently high numbers to interact. The second phase is that of "interactive species equilibrium", the logical extension of the first phase. As populations of species increase unimpeded by others (phase 1), they ultimately reach a point in time where contact with other species is inevitable. During this phase, interspecific contact and the potential for interaction are realized. The third phase, "assortative species equilibrium" is one of continued colonization and interaction. During this phase, the species which are more adapted to the peculiarities of the particular environment, or which can effectively co-exist with the other species in that environment, persist. The final phase is the "evolutionary species equilibrium". Wilson suggests that if a community persists a sufficient length of time, the species will adapt to each other as well as to the environment.

Two of the phases, the first and last, are non-interactive. The first by definition, the last by implication (coevolution). Note that both the hypothesis of Holmes (1973) and that of Price (1980) fit into the scheme

of Wilson (1969) but at opposite ends of the spectrum. Holmes' selective site selection is a restatement, for helminths, of an evolutionary species equilibrium whereas Price's colonization by specialists is a restatement, for parasites in general, of a non-interactive species equilibrium.

Results from the current study do not provide exclusive support to either hypothesis. There appear to be two components comprising the infracommunities in lesser scaup: the frequent, abundant species and the moderately frequent, scarce or infrequent, scarce species. Species comprising the former component occupy predictable, sequential positions; are not randomly distributed; and show negligible niche overlap with each other. In short, they fit the pattern envisaged by Wilson (1969) for an evolutionary species equilibrium; in the terminology of Holmes (1973), they may be species exhibiting selective site segregation. However, results from the current study show more of an intermediary pattern than suggested by Holmes (1973). He concluded that selective site selection was much more common than interactive site selection. His conclusions were based on published studies that did not provide the same detail as the present study. The current data do suggest that the frequent species are largely selective but with some interactive segregation. Based on available evidence, these species are either specialists to scaup or extreme generalists to waterfowl. Species in the latter component

show less predictability in location, may be randomly distributed, and show considerably higher niche overlap with other species. They fit Wilson's first pattern of non-interactive species equilibrium; in Price's (1980) terminology they represent chance colonization by specialists. Based on available evidence, these are species that are specialists to other hosts. Furthermore, where known, the evidence suggests that these species invade scaup by using preferred food items of lesser scaup.

In summary, evidence from these infracommunities in lesser scaup concurrently support the hypothesis of Holmes (1973) and that of Price (1980), suggesting that observed community structure may, in fact, be the result of a multiplicity of independently operating mechanisms. The frequent and abundant species appear to be coevolved (or coevolving) species, at (or past) the stage of competitive interaction, evolving (or having evolved) selective site selection to permit coexistence. These are species which appear to have a long evolutionary history with waterfowl in general or lesser scaup in particular. The remaining species appear to be specialists from other hosts, acting as invasive colonists in lesser scaup.

VIII. Concluding Remarks

Traditionally, questions relating to faunal similarity and those relating to community structure are treated as independent subjects. That is the treatment they have received in the current thesis. However, the data presented here suggest that the two approaches should be integrated more thoroughly. In fact, the data suggest that the emphasis should be placed on comparing the deterministic versus the stochastic components. This conclusion, that community structure is the result of mechanisms at opposite poles of an evolutionary sequence, has some interesting implications to fundamental community theory (discussed below).

Although most features distinguishing deterministic and stochastic groups were addressed explicitly, others were only implied. Therefore, a further examination of these two groups, using anecdotal evidence (where possible) to supplement statistical evidence presented earlier, is warranted. Table 12 presents a comparison showing the characteristics of these two groups of components.

The deterministic species were frequent, the stochastic species were not frequent. Abundance relationships within and between the groups were variable. Most of the deterministic species were abundant, most stochastic species were not. However, on occasion, the average (and total) number of individuals in the stochastic species was greater than in a deterministic species (e.g., compare n and N between L. skrjabini [deterministic] and Unciunia n. sp.

Table 12. Characteristics of the deterministic and stochastic components in lesser scaup

Influencing factors		
Characteristic	Deterministic	Stochastic
Numbers	Frequent and usually abundant	Infrequent, on occasion abundant
Similarity	Provide similarity between samples	Provide no similarity
Stability	Evidence for persistence stability	No evidence for persistence stability
Specificity	Generalists in waterfowl or specialists in lesser scaup	Specialists in other hosts
Interaction	Low niche overlap	High niche overlap
Distribution	Not randomly distributed	Randomly distributed
Evolutionary		
Phase*	3 or 4	1 or 2

* of Wilson (1969)

[stochastic] in Table 5). In an extreme example, an infrequent species, "CC" ($n=2$), was very abundant (mean=1990). These data suggest that, given sufficient replicates, frequency (and not abundance) is the more important variable in differentiating between deterministic and stochastic species.

Related to frequency and abundance, the deterministic group provides the similarity between samples. The stochastic group adds little to that similarity. The results of discriminant function analysis suggested that the most discriminating variables were the relative abundances of some frequent species followed by the presence/absence of some infrequent species. Further examination of the mean abundances of the species suggested that the most discriminating, frequent species provided good separation of clusters. Furthermore, the overall similarity among the samples was quite high. For example, considering the entire dataset of 59 variables, a single cluster is formed at slightly less ($r=-0.069$) than 50% similarity ($r=0.0$). Considering only species occurring in more than 5 infracommunities (which still includes some stochastic species), a single cluster is formed at $r=-0.093$. Thus the difference attributable to those species occurring in less than 5 infracommunities is negligible. The same comparison for the 10 recurrent group species (no stochastic species) shows a single cluster formed at $r=-0.142$, further emphasizing what little impact the stochastic group has on

faunal similarity.

Evidence for persistence stability in the deterministic group was presented earlier. The lack of persistence stability in the stochastic group was not specifically addressed. In comparing the infrequent species between the three surveys on adult scaup helminth faunas, only those species for which there is no possibility for taxonomic inconsistencies are considered. Graham (1966) found 11 infrequent species in 135 birds, Hair (1975) found 12 in 30 birds, I found 30 in 45 birds. However, there was only one species found in all three studies, three in common between Graham and Hair, three between Graham and mine, and three between Hair and mine. A total of 53 infrequent species was found in the three studies. In short, even with this conservative approach, most of the infrequent species were found in only one study, frequently in only one infracommunity from that study. Based on this evidence, it would be hard to consider persistence stability as one of the characteristics of the infrequent species.

Three of the deterministic species, F. fasciolaris, Dic. coronula, and A. gracilis, represent examples of the most extreme generalists known to infect waterfowl (McDonald, 1969). The inclusion of generalists in the deterministic group runs counter to some current assumptions. For example, Holmes and Price (1980) suggest that most parasite communities will contain generalists, not part of any coevolved subunit. Their two arguments leading

to that conclusion were: significant coevolution should occur only where parasites co-occur regularly and parasite communities might be expected to evolve as subunits. Two of the three species mentioned above, F. fasciolaris and A. gracilis, are very frequent and co-occur regularly among themselves and with other deterministic species. At least one of these, F. fasciolaris, can also use the same intermediate hosts as the very frequent and abundant scaup specialists; thus the potential for others to coevolve with it is great. Whether it coevolves equally with them may be diluted by evolutionary pressures on infrapopulations in other host species.

Deterministic species have low niche overlap values suggesting different niche exploitation patterns. Obvious exceptions come, not from the current dataset, but from data in Hair and Holmes (1975). The diagrams in Figure 3 of Hair and Holmes (p. 264) show large (first diagram) and complete (second diagram) overlap between H. spinocirrosa and H. abortiva. Frankly, I cannot explain those overlaps. In the remaining eight infracommunities from that study, in the 82 (includes 52 ducklings) infracommunities in a later study (Hair, 1975), and in the 45 infracommunities in the current study, that degree of overlap was never seen again. In the current study, the fundamental overlap between those species was 21% and the realized overlap was only 5%. Appendix 14 shows the actual distributions of all of the species comprising the microsomacanthid "species flock" for each

infracommunity. I have to conclude that the extreme overlaps referred to are either errors in the data (these were the first birds examined by Hair) or they may be the "rare event" Price (1980) challenges us to study. In contrast to the low overlaps among the deterministic species, overlaps among the stochastic species were high. This suggests that these species occupy very similar niches (at least in terms of the linear component). Holmes and Price (1980) provide a possible explanation: if these stochastic species rely on rapidly replenished resources, they may coexist in exceedingly similar niches. Extending this idea to all species in the gut, the generalist species in the deterministic group may require some resource or condition common to all waterfowl whereas the lesser scaup specialists may require a resource or condition common to lesser scaup, but rare in other waterfowl. The stochastic species, which are specialists in other hosts, may require resources or conditions characteristic of those hosts but rare in scaup. Because these rare resources or conditions are not used by most species in the gut, they would be difficult to differentiate from a rapidly replenished resource. Unfortunately, these ideas will remain untestable until such time as we know more about the physiology of each helminth (and host) species.

The deterministic species are not randomly distributed along the gut. Their sequence of distributions are not only highly predictable, they appear to be highly correlated with

particular locations along the gut. Although the mean distances cannot be differentiated from predicted random distances, the standard deviations of those distances are significantly less than predicted, suggesting much greater regularity in distribution. On the other hand, the stochastic species, frequently represented by one or two individuals in one or two infracommunities, could not be differentiated from random.

There is a strong tendency among others who disclaim predation as an organizing force (cf. Brown, 1975; Diamond, 1975; Pianka, 1975; to name but a few), to invoke competition as the single structuring mechanism in their systems. Such a simplistic explanation will not explain the variance in the current analyses. The current data suggest a multiplicity of mechanisms responsible for producing the observed structure in the helminth infracommunities of lesser scaup. The variance in the data also suggest that it would be difficult to differentiate discrete phases as suggested by Wilson (1969). As such, the deterministic species appear to be those assignable to either phase 3 or 4 in Wilson's scheme; absolute differentiation between the two is difficult without experimentation. In the same vein, the stochastic species appear to be those in phase 1 or 2; the differentiation between these two phases being confounded because the species occurrences are rare events.

I began with a statement by Peter Price suggesting that the time is ripe for speculation in parasite ecology. I

would be remiss if I did not accept that challenge (as if no speculation precedes this!). However, I would suggest that when we know enough about the helminth faunas of all hosts in a given area, we will find that all four evolutionary phases in community development envisaged by Wilson (1969) act concurrently and synergistically to produce the structure that we observe. And that neither Holmes (1973) nor Price (1980) are entirely correct in hypothesizing such encompassing ideas as "helminth communities are mature" or that "parasite communities are young". Furthermore, if we are careful in the analyses we do, and the records we leave behind, those that follow us cannot but conclude that the helminth communities are dynamic, evolving systems and not the static assemblages we portray them to be.

In closing, I will borrow a quote from Holmes and Price (1980) "It is too early to be an emphatic proponent of any one hypothesis".

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Appendix 1. Data matrix of helminth species and locations along resource continuum for each individual sample used in analyses.

Key to Appendix 1.

Helminth Species (Row number)

- | | |
|---------------------------------------|-------------------------------------|
| 1. <u>Fimbriaria fasciolaris</u> | 27. <u>Retinometra cyrtoides</u> |
| 2. <u>Hymenolepis spinocirrosa</u> | 28. "U" |
| 3. <u>H. abortiva</u> | 29. <u>H. melanittae</u> |
| 4. <u>H. pusilla</u> | 30. <u>Oligorchis n. sp.</u> |
| 5. <u>H. tuvensis</u> | 31. <u>Diorchis inflata</u> |
| 6. <u>Tuensis A</u> | 32. "W" |
| 7. <u>Echinoparyphium recurvata</u> | 33. "P" |
| 8. <u>Apatemon gracilis</u> | 34. "X" |
| 9. <u>Lateriporus skrjabini</u> | 35. "Y" |
| 10. <u>Retinometra pittalugai</u> | 36. "Z" |
| 11. <u>Polymorphus marilis</u> | 37. "AA" |
| 12. <u>Dicranotaenia coronula</u> | 38. "J" |
| 13. <u>H. recurvata</u> | 39. "y" |
| 14. <u>H. recurvata</u> | 40. <u>H. albertensis</u> |
| 15. <u>H. microskrjabini</u> | 41. <u>Strongyloides sp.</u> |
| 16. <u>Sobolevicanthus kenafensis</u> | 42. "K" |
| 17. <u>H. parvula</u> | 43. "N" |
| 18. <u>Cotylurus hebraicus</u> | 44. <u>Sobolevicanthus gracilis</u> |
| 19. <u>H. fausti</u> | 45. "I" |
| 20. <u>Corynosoma constrictum</u> | 46. "DD" |
| 21. <u>Capillaria obsignata</u> | 47. "S" |
| 22. <u>H. arcuata</u> | 48. "FF" |
| 23. <u>H. arcuata</u> | 49. "GG" |
| 24. <u>Diorchis n. sp.</u> | 50. "HH" |
| 25. <u>Hymenolepis sp. 1</u> | 51. "I" |
| 26. <u>Hymenolepis sp. 2</u> | 52. "J" |

Key to Appendix 1. (continued)

Intestinal Section (Column number)

Section 1 begins at junction of small intestine and gizzard.

Section 20 ends at junction of small intestine and large intestine.

Bird Numbers

- 1-3: Iosegun Lake samples 1-3.
- 4-6: Murray Lake samples 1-3.
- 7-9: Rattlesnake Lake (1977) samples 1-3.
- 10-12: Rattlesnake Lake (1978) samples 1-3.
- 13-15: Bistcho Lake samples 1-3.
- 16-18: Dusty Lake samples 1-3.
- 19-21: Charron Lake samples 1-3.
- 22-24: Chip Lake samples 1-3.
- 25-27: Lanes Lake samples 1-3.
- 28-30: Wolf Lake samples 1-3.
- 31-33: Tyrrell Lake samples 1-3.
- 34-36: Bellshill Lake samples 1-3.
- 37-39: Cowoki Lake samples 1-3.
- 40-45: Fleecinghorse Lake samples 1-6.

[illegible]

TABLE		BIRD 15	
1	0	1	0
2	0	2	0
3	0	3	0
4	0	4	0
5	0	5	0
6	0	6	0
7	0	7	0
8	0	8	0
9	0	9	0
10	0	10	0
11	0	11	0
12	0	12	0
13	0	13	0
14	0	14	0
15	0	15	0
16	0	16	0
17	0	17	0
18	0	18	0
19	0	19	0
20	0	20	0
21	0	21	0
22	0	22	0
23	0	23	0
24	0	24	0
25	0	25	0
26	0	26	0
27	0	27	0
28	0	28	0
29	0	29	0
30	0	30	0
31	0	31	0
32	0	32	0
33	0	33	0
34	0	34	0
35	0	35	0
36	0	36	0
37	0	37	0
38	0	38	0
39	0	39	0
40	0	40	0
41	0	41	0
42	0	42	0
43	0	43	0
44	0	44	0
45	0	45	0
46	0	46	0
47	0	47	0
48	0	48	0
49	0	49	0
50	0	50	0
51	0	51	0
52	0	52	0

TABLE		BIRD 23	
1	1	17	1
2	2	20	2
3	3	20	3
4	4	20	4
5	5	20	5
6	6	20	6
7	7	20	7
8	8	20	8
9	9	20	9
10	10	20	10
11	11	20	11
12	12	20	12
13	13	20	13
14	14	20	14
15	15	20	15
16	16	20	16
17	17	20	17
18	18	20	18
19	19	20	19
20	20	20	20
21	21	20	21
22	22	20	22
23	23	20	23
24	24	20	24
25	25	20	25
26	26	20	26
27	27	20	27
28	28	20	28
29	29	20	29
30	30	20	30
31	31	20	31
32	32	20	32
33	33	20	33
34	34	20	34
35	35	20	35
36	36	20	36
37	37	20	37
38	38	20	38
39	39	20	39
40	40	20	40
41	41	20	41
42	42	20	42
43	43	20	43
44	44	20	44
45	45	20	45
46	46	20	46
47	47	20	47
48	48	20	48
49	49	20	49
50	50	20	50
51	51	20	51
52	52	20	52

TABLE		BIRD 26	
1	0	0	0
2	0	0	0
3	0	0	0
4	0	0	0
5	0	0	0
6	0	0	0
7	0	0	0
8	0	0	0
9	0	0	0
10	0	0	0
11	0	0	0
12	0	0	0
13	0	0	0
14	0	0	0
15	0	0	0
16	0	0	0
17	0	0	0
18	0	0	0
19	0	0	0
20	0	0	0
21	0	0	0
22	0	0	0
23	0	0	0
24	0	0	0
25	0	0	0
26	0	0	0
27	0	0	0
28	0	0	0
29	0	0	0
30	0	0	0
31	0	0	0
32	0	0	0
33	0	0	0
34	0	0	0
35	0	0	0
36	0	0	0
37	0	0	0
38	0	0	0
39	0	0	0
40	0	0	0
41	0	0	0
42	0	0	0
43	0	0	0
44	0	0	0
45	0	0	0
46	0	0	0
47	0	0	0
48	0	0	0
49	0	0	0
50	0	0	0
51	0	0	0
52	0	0	0

TABLE		BIRD 34	
1	0	0	0
2	0	0	0
3	0	0	0
4	0	0	0
5	0	0	0
6	0	0	0
7	0	0	0
8	0	0	0
9	0	0	0
10	0	0	0
11	0	0	0
12	0	0	0
13	0	0	0
14	0	0	0
15	0	0	0
16	0	0	0
17	0	0	0
18	0	0	0
19	0	0	0
20	0	0	0
21	0	0	0
22	0	0	0
23	0	0	0
24	0	0	0
25	0	0	0
26	0	0	0
27	0	0	0
28	0	0	0
29	0	0	0
30	0	0	0
31	0	0	0
32	0	0	0
33	0	0	0
34	0	0	0
35	0	0	0
36	0	0	0
37	0	0	0
38	0	0	0
39	0	0	0
40	0	0	0
41	0	0	0
42	0	0	0
43	0	0	0
44	0	0	0
45	0	0	0
46	0	0	0
47	0	0	0
48	0	0	0
49	0	0	0
50	0	0	0
51	0	0	0
52	0	0	0

Appendix 2. Taxonomic characters of helminth species that could not be identified. Terminology for hook shape follows Czaplinski (1956). Hook lengths are in micrometers.

Designation	Hooks		Remarks
	Number (Length)	Hook Shape	
"O"	8 (100)	Skrjabini	-
"I"	10 (67)	Diorchid	Large intestine
"W"	10 (30-31)	Diorchid	-
"F"	8 (48)	Skrjabini	<u>Soboleviancanthus</u> (?)
"X"	10 (58)	Diorchid a	-
"CC"		Diorchid a	
"Z"	10 (88)	Diorchid a	-
"A"	10 (31)	Arcuatus	-
"FE"	9? (64)	Diorchid a	Armed suckers
"J"	22 (11.5)	Aploparakis	-
"Y"	10 (46-48)	Arcuatus	Spined cirrus
"K"	10 (113-115)	Diorchid	-
"N"	10 (30-31)	Diorchid a	Spined cirrus
"T"	10 (26-27)	Diorchid	-
"DD"	10 (79)	Diorchid	Armed suckers
"KK"	12 (176)	Skrjabini	-
"L"	10 (43-46)	Diorchid	-
"GG"	10 (20)	Diorchid a	-
"HH"	8 (56-58)	Skrjabini	-
"II"	10 (29)	Diorchid	-
"JJ"	10 (106)	Diorchid a	Armed suckers
<u>Diorchis</u> n. sp.	10 (38-44)	Diorchid	Hooks identical to <u>ransomi</u>
<u>Oligorchis</u> n. sp.	See Graham (1966)		
<u>Unciunia</u> n. sp.	none		Immature
<u>Hymenolepis</u> sp. 1	10 (58-62)	Diorchid	3 testes, <u>Myxolepis</u> (?)
<u>Hymenolepis</u> sp. 2	10 (26-28)	Diorchid	3 testes, cirrus armed for distal 1/3

Appendix 3. Average ranks from Kruskal-Wallis test between abundances of the 16 most frequent species. Comparisons are between the 4 clusters produced from the 59 variable dataset.

Species	Cluster				p=
	1	2	3	4	
<u>Fimbriaria fasciolaris</u>	33	24	21	15	.04
<u>Hymenolepis spinocirrosa</u>	36	24	26	8	.00
<u>H. abortiva</u>	35	24	27	8	.00
<u>H. pusilla</u>	33	25	26	9	.00
<u>H. tuvensis</u>	32	32	10	15	.00
Tuvenis A	21	21	32	18	.05
<u>Echinoparyphium recurvatum</u>	27	22	23	21	.77
<u>Apatemon gracilis</u>	17	24	23	26	.57
<u>Lateriporus skrjabini</u>	23	27	20	20	.47
<u>Retinometra pittalugai</u>	31	19	29	17	.03
<u>Polymorphus marilis</u>	26	25	24	17	.33
<u>Dicranotaenia coronula</u>	33	13	28	26	.00
<u>H. recurvata</u>	22	22	24	24	.96
<u>H. microskrjabini</u>	22	31	17	18	.02
<u>Cotylurus hebraicus</u>	18	26	26	20	.39
<u>Corynosoma constrictum</u>	29	21	26	19	.33

Appendix 4. Average ranks from Kruskal-Wallis test between abundances of the 16 most frequent species. Comparisons are between the 4 clusters produced from the 29 variable dataset.

Species	Cluster				p=
	1	2	3	4	
<u>Fimbriaria fasciolaris</u>	26	26	18	15	.17
<u>Hymenolepis spinocirrosa</u>	32	24	12	21	.00
<u>H. abortiva</u>	32	24	12	22	.00
<u>H. pusilla</u>	28	26	14	23	.03
<u>H. tuvensis</u>	21	31	15	25	.01
Tuvensis A	27	21	21	26	.53
<u>Echinoparyphium recurvatum</u>	25	23	20	28	.75
<u>Apatemon gracilis</u>	16	26	28	21	.07
<u>Lateriporus skrjabini</u>	23	28	19	16	.15
<u>Retinometra pittalugai</u>	28	19	22	23	.27
<u>Polymorphus marilis</u>	28	26	15	18	.05
<u>Dicranotaenia coronula</u>	28	15	28	18	.02
<u>H. recurvata</u>	20	24	26	22	.72
<u>H. microskrjabini</u>	19	32	19	15	.01
<u>Cotylurus hebraicus</u>	17	28	25	20	.14
<u>Corynosoma constrictum</u>	28	23	19	20	.36

Appendix 5. Average ranks from Kruskal-Wallis test between abundances of the recurrent group species. Comparisons are between the 4 clusters produced from the 10 variable dataset.

Species	Cluster				p=
	1	2	3	4	
<u>Fimbriaria fasciolaris</u>	30	16	21	19	.02
<u>Hymenolepis spinocirrosa</u>	26	9	26	31	.00
<u>H. abortiva</u>	26	9	27	30	.00
<u>H. pusilla</u>	26	10	25	32	.00
<u>H. tuvensis</u>	29	21	13	29	.01
Tuvenis A	11	25	31	30	.00
<u>Apatemon gracilis</u>	19	35	18	18	.01
<u>Retinometra pittalugai</u>	28	18	27	11	.02
<u>Polymorphus marilis</u>	24	14	29	20	.04
<u>Dicranotaenia coronula</u>	21	23	28	16	.23

Appendix 6. Results of principal-component analysis based on all helminth species occurring in more than 5 samples.

EIGENVALUES

4.98 3.75 2.47 2.38 1.91 1.69 1.51 1.42 1.25 1.14 0.85 0.78 0.72 0.63 0.53 0.48
0.42 0.40 0.31 0.25 0.19 0.17 0.15 0.10 0.09 0.06 0.04 0.02

CUMULATIVE VARIANCE

17.19 12.92 8.52 8.22 6.58 5.83 5.21 4.89 4.31 3.94 2.95 2.69 2.47 2.16 1.83 1.67
1.26 1.26 1.16 0.89 0.83 0.67 0.60 0.52 0.35 0.31 0.22 0.15 0.08

CUMULATIVE VARIANCE

17.19 30.11 38.63 45.84 52.42 58.25 64.46 69.35 73.65 77.60 80.55 83.24 85.72 87.87 89.70 91.37
92.82 94.20 95.58 96.87 98.10 99.77 99.89 99.92 99.92 99.92 99.92 99.92 99.92 99.92 99.92 99.92

EIGENVECTORS - BY ROWS

VECTOR 1 0.305 0.370 0.354 0.371 0.133 0.161 0.191 0.069 0.143 0.233 0.220 0.187 0.031 0.100 0.044 0.111 0.251 0.078
0.073 0.093 0.030 0.078 0.133 0.233 0.106 0.146 0.054 0.203 0.041
VECTOR 2 -0.116 0.110 0.107 0.116 0.050 0.079 0.126 0.165 0.231 0.109 0.138 0.238 0.280 0.128 0.170 0.032 0.037 0.075
0.170 0.132 0.088 0.351 0.358 0.176 0.298 0.040 0.235 0.250 0.290
VECTOR 3 -0.094 0.027 0.036 0.005 0.270 0.097 0.129 0.132 0.122 0.002 0.181 0.008 0.208 0.166 0.074 0.252 0.188 0.372
0.230 0.347 0.269 0.242 0.127 0.125 0.249 0.170 0.265 0.107 0.076
VECTOR 4 0.267 0.105 0.169 0.060 0.349 0.212 0.053 0.161 0.202 0.021 0.058 0.102 0.026 0.386 0.348 0.347 0.104 0.146
0.169 0.104 0.020 0.089 0.013 0.074 0.057 0.352 0.168 0.032 0.070

EIGENVECTORS - BY COLUMNS

S 1 0.293 0.765 0.155 -1.071 S 24 2.370 0.036 -2.563 -0.679
S 2 0.402 0.918 0.339 0.264 S 25 -0.814 -1.819 -0.179 4.025
S 3 1.088 0.851 0.475 1.553 S 26 -0.141 -1.143 0.850 -0.921
S 4 -0.513 -1.203 0.263 -0.691 S 27 2.061 -2.202 0.967 2.250
S 5 -1.708 0.470 1.084 1.239 S 28 -0.549 -0.750 0.192 0.848
S 6 0.021 -1.080 0.728 0.703 S 29 0.322 -1.113 -1.273 -1.621
S 7 5.016 4.462 2.845 0.240 S 30 -0.920 -0.412 0.021 -1.216
S 8 2.568 2.971 4.310 1.507 S 31 -0.875 0.582 0.336 -1.615
S 9 -0.990 0.841 3.053 -0.302 S 32 -1.285 0.940 0.571 -0.776
S 10 -3.837 1.057 -1.328 0.700 S 33 0.161 -0.316 -1.806 1.016
S 11 -1.718 0.726 0.245 -2.146 S 34 -1.009 3.752 0.919 2.278
S 12 -2.306 1.903 -1.963 0.544 S 35 0.436 -2.421 -0.617 1.522
S 13 1.320 7.350 -2.630 -1.565 S 36 1.727 2.059 -2.726 -0.093
S 14 -0.331 0.967 1.866 -3.299 S 37 -0.546 -1.476 -0.711 0.503
S 15 0.218 0.695 1.572 -3.367 S 38 1.209 -2.007 -1.011 0.117
S 16 -0.759 0.433 0.322 -0.795 S 39 0.443 -0.945 0.893 1.204
S 17 0.863 -2.205 -1.459 1.905 S 40 -1.693 -0.116 1.749 -0.246
S 18 0.023 1.892 0.467 1.997 S 41 -4.047 0.818 0.288 -0.401
S 19 3.335 0.373 -2.918 0.072 S 42 -7.121 1.506 -1.507 -0.404
S 20 4.149 0.980 0.495 -3.308 S 43 -3.075 2.592 -0.096 1.748
S 21 4.663 0.051 -2.917 0.060 S 44 -1.281 1.185 0.207 0.125
S 22 1.258 0.948 1.971 0.990 S 45 -0.082 -0.071 0.116 1.273
S 23 1.555 -1.951 0.792 0.300

Appendix 7. Results of principal-component analysis on all helminth species comprising the recurrent group.

EIGENVALUES

3.66	1.53	1.20	0.97	0.89	0.59	0.54	0.35	0.19	0.08
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PERCENTAGE VARIANCE

36.61	15.32	11.96	9.72	8.87	5.87	5.42	3.52	1.87	0.83
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CUMULATIVE VARIANCE

36.61	51.93	63.89	73.61	82.48	88.35	93.77	97.30	99.16	100.00
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EIGENVECTORS - BY ROWS

VECTOR	1	0.352	0.459	0.461	0.468	0.190	0.170	0.040	0.248	0.258	0.197
VECTOR	2	0.115	0.075	-0.018	-0.000	0.258	-0.519	-0.576	0.096	0.262	-0.485
VECTOR	3	0.278	-0.051	-0.161	-0.059	0.688	-0.214	0.534	0.019	-0.270	-0.117

FIRST 4 FACTOR SCORES

S 1	0.855	0.108	-0.759	1.176	S 31	-0.477	-0.933	-1.067	0.011
S 2	1.129	0.600	-0.071	0.359	S 32	-0.566	-0.510	0.580	-1.351
S 3	0.890	0.489	0.674	-1.234	S 33	0.395	2.062	0.665	2.007
S 4	-0.236	-0.395	0.353	-0.761	S 34	-2.289	-1.734	0.841	0.442
S 5	-1.673	-0.781	1.544	-0.925	S 35	0.720	2.005	0.052	0.643
S 6	0.224	-0.550	2.067	1.632	S 36	2.003	-0.933	0.184	0.798
S 7	2.883	-1.384	-0.443	1.438	S 37	-0.415	1.387	0.724	-1.013
S 8	1.678	-0.774	0.382	1.178	S 38	1.006	-0.363	0.198	-2.136
S 9	-1.255	-3.039	0.174	1.356	S 39	0.466	0.444	1.362	-0.337
S 10	-4.266	0.660	0.088	-0.053	S 40	-1.684	0.445	-0.285	-0.021
S 11	-1.149	-0.084	-2.223	-0.046	S 41	-4.069	1.078	-1.495	0.123
S 12	-1.854	-2.163	0.605	-0.540	S 42	-5.927	1.156	-0.868	0.479
S 13	0.200	-0.496	-0.387	0.974	S 43	-2.475	-1.173	0.647	0.931
S 14	-0.407	0.621	-0.756	0.476	S 44	-0.549	-1.372	0.911	1.454
S 15	0.067	-0.766	-2.765	-0.320	S 45	-0.112	-0.261	0.893	0.697
S 16	0.340	0.485	-0.140	1.457					
S 17	0.928	2.368	0.040	0.585					
S 18	-0.177	-0.476	1.137	-0.771					
S 19	2.804	0.056	0.967	1.181					
S 20	2.854	-1.218	-2.111	0.326					
S 21	3.328	-0.257	0.004	0.318					
S 22	1.057	-1.219	1.006	0.322					
S 23	1.920	2.981	0.510	0.047					
S 24	2.400	0.627	0.783	0.959					
S 25	-1.414	1.934	1.467	0.574					
S 26	0.171	-0.101	2.744	-1.054					
S 27	2.026	0.219	0.399	1.846					
S 28	-0.290	-0.087	1.075	0.331					
S 29	1.285	0.524	-0.960	-1.096					
S 30	-0.342	0.658	-0.226	0.641					

Appendix 8. 52 x 52 matrix of the average symmetrical overlap (percent similarity) between species. Species codes same as Appendix 1.

[illegible]

Appendix 9. 52 x 52 matrix of the standard deviation of average symmetrical overlap (percent similarity) between species. Species codes as in Appendix 1.

Appendix 10. 52 x 52 matrix of summed, symmetrical overlap (percent similarity) between species. Bird 46 was created by adding bird 1 to bird 2 to....bird 45. Species codes same as Appendix 1.

Appendix 11. 52 x 52 matrix of the average asymmetrical overlap (Levins, 1968) between species.
Species codes same as Appendix 1.

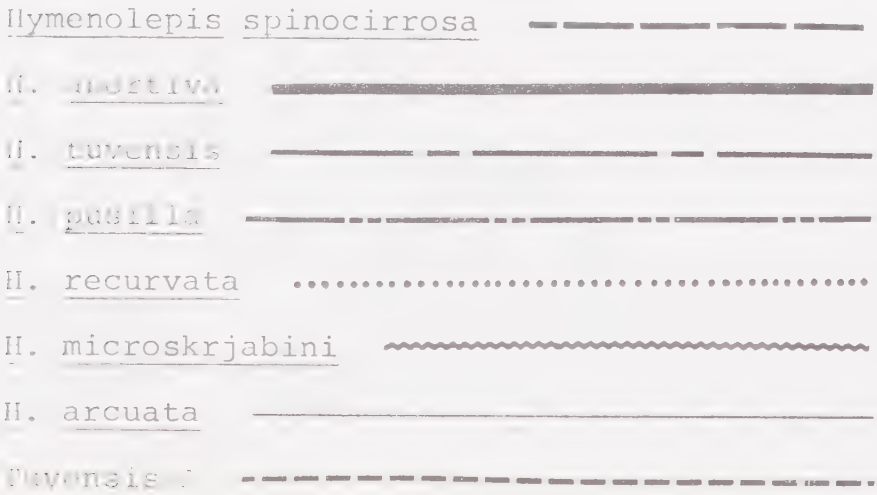
Appendix 12. 52 x 52 matrix of the standard deviation of average, asymmetrical overlap (Levins, 1968) between species. Species codes same as Appendix 1.

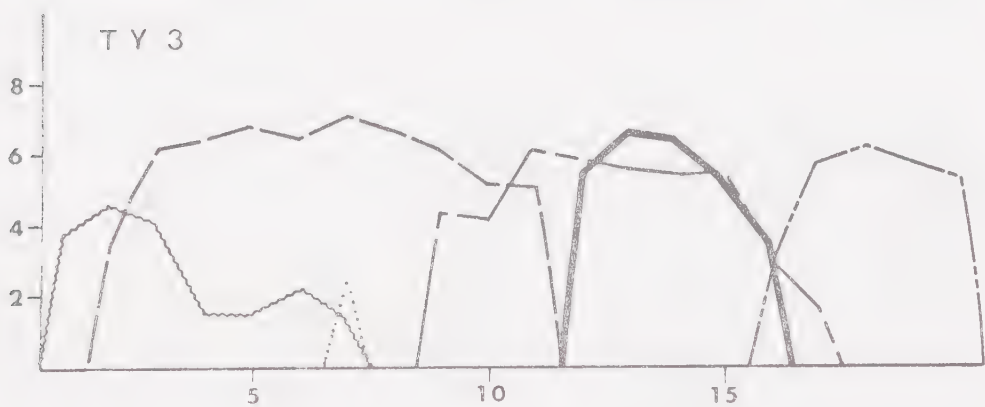
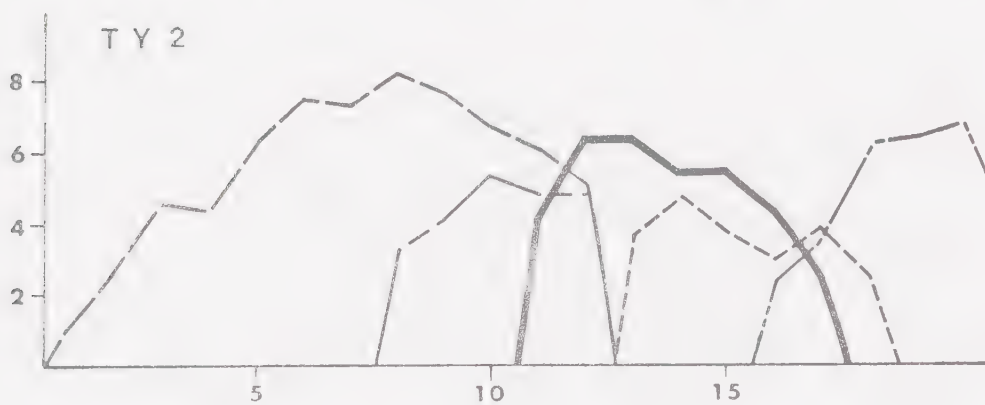
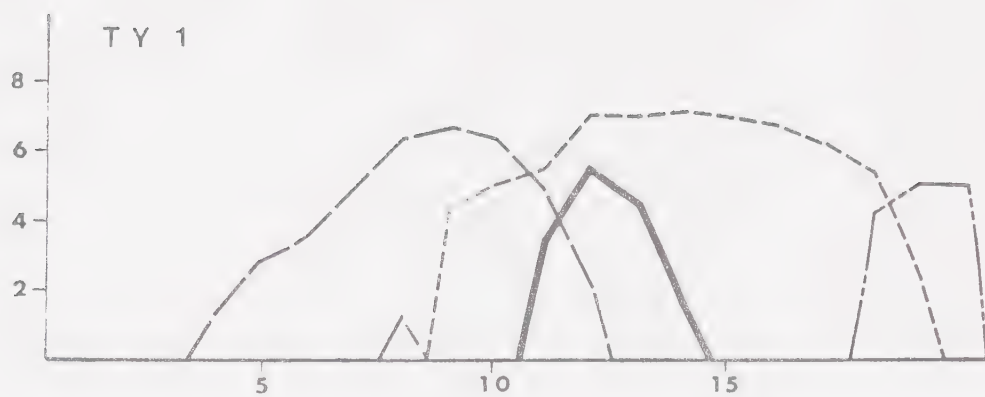
Appendix 13. 52 x 52 matrix of summed asymmetrical overlap (Levins, 1968) between species. Bird 46 was created by adding bird 1 to bird 2 to....bird 45. Species codes same as Appendix 1.

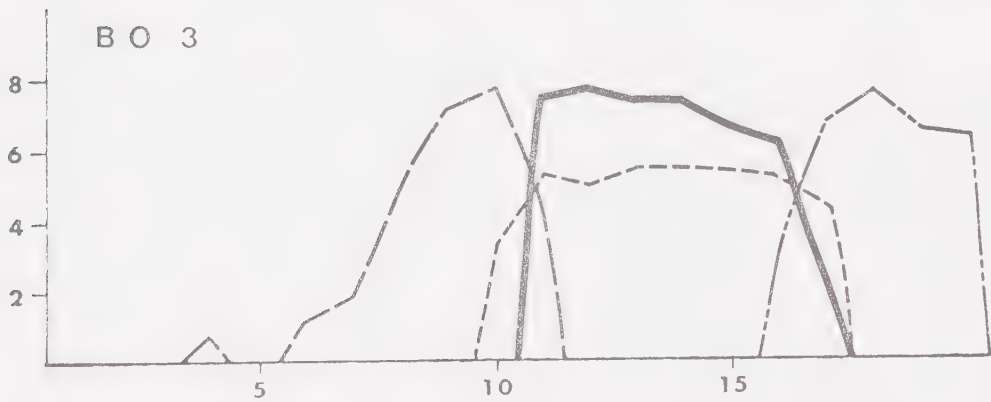
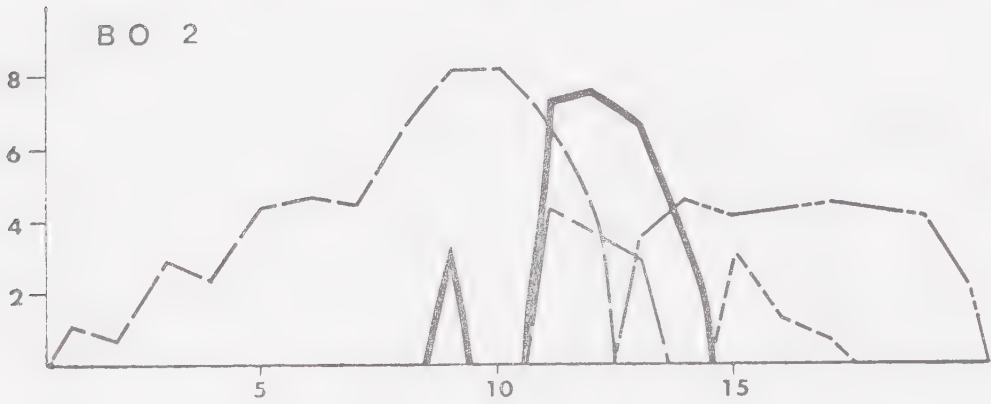
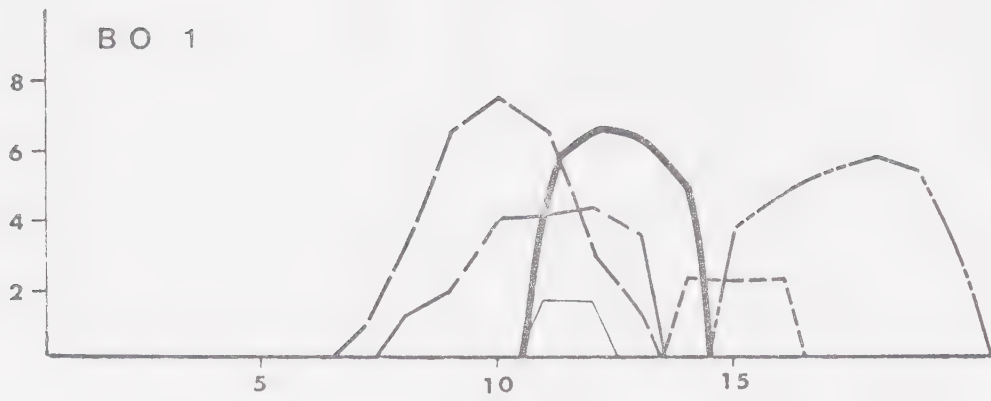
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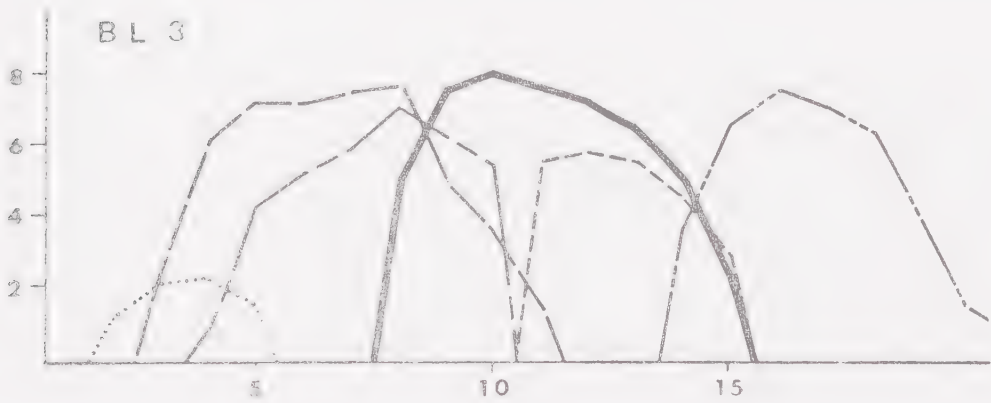
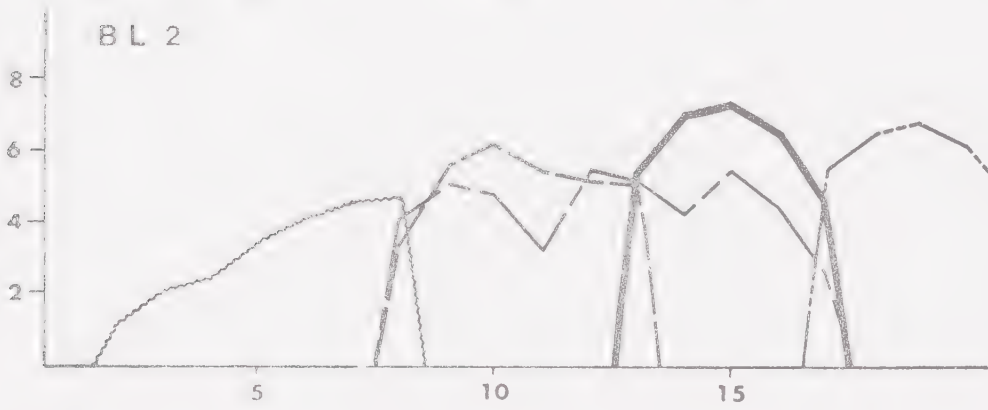
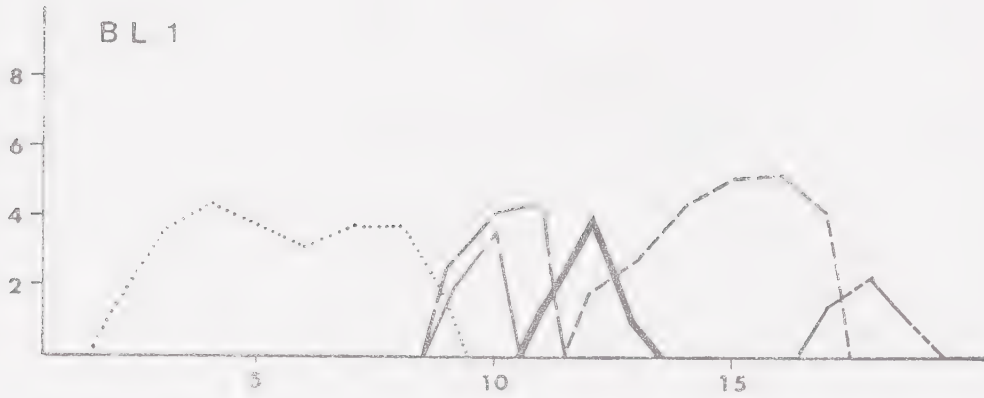
Appendix 14. Actual population size and distribution of each of the hymenolepid species comprising the largest species flock. Because of the uncertain status of *Tuvensis* A and because of its similarity to other members of the subgenus Microsomacanthus, it is included for comparative purposes. See text for further discussion.

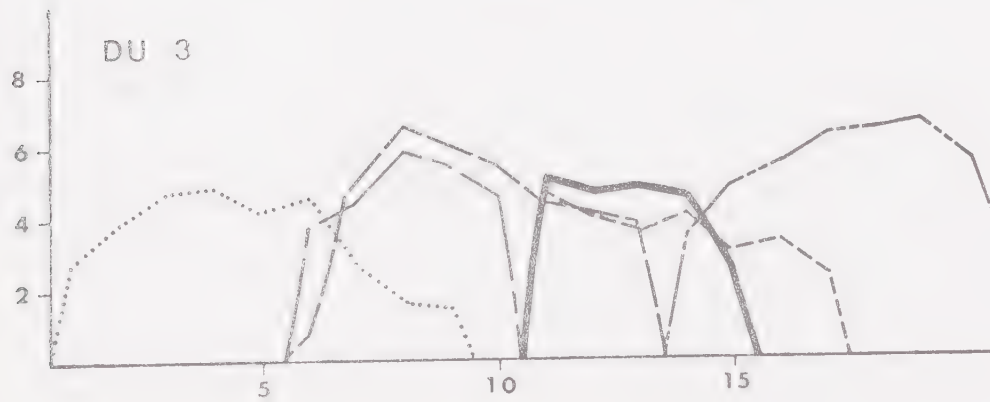
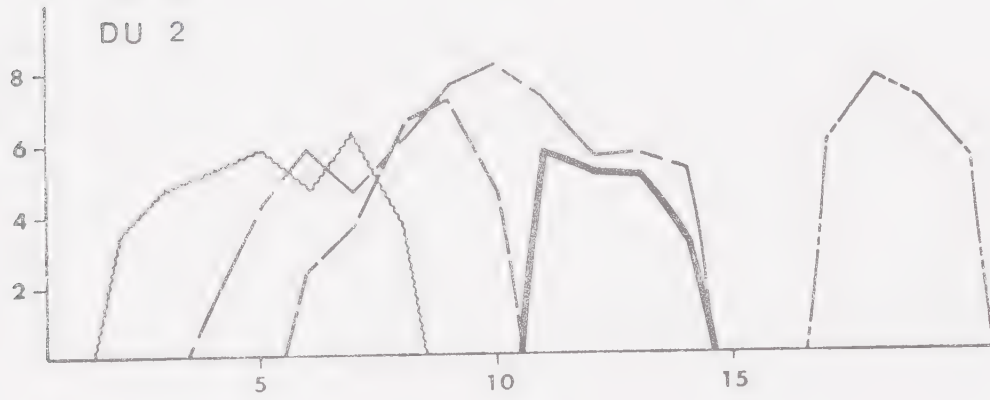
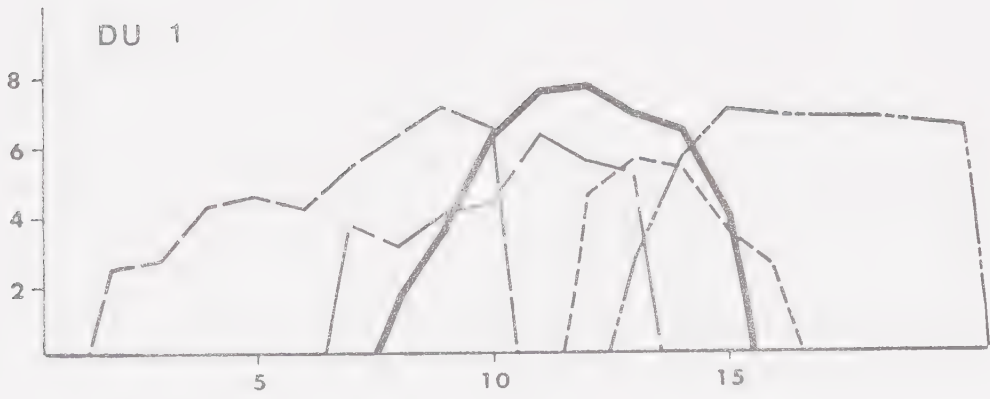
Key: Population sizes are given as the Ln of the number of individuals within a section. The X-axis represents the resource continuum for the sample.

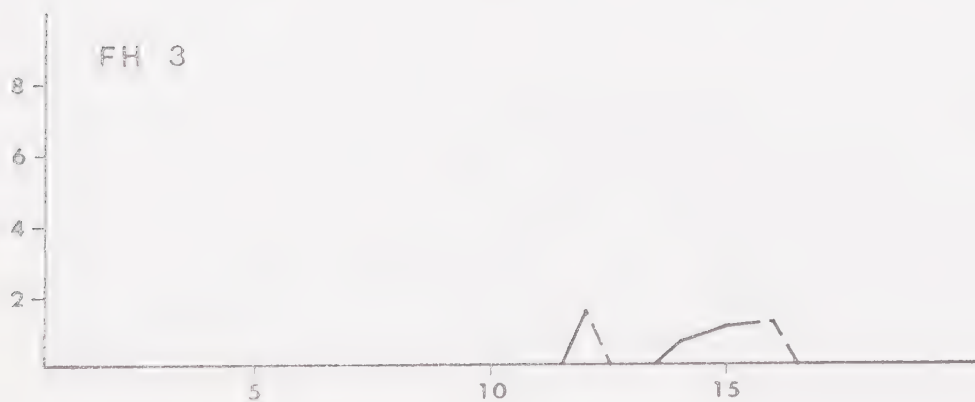
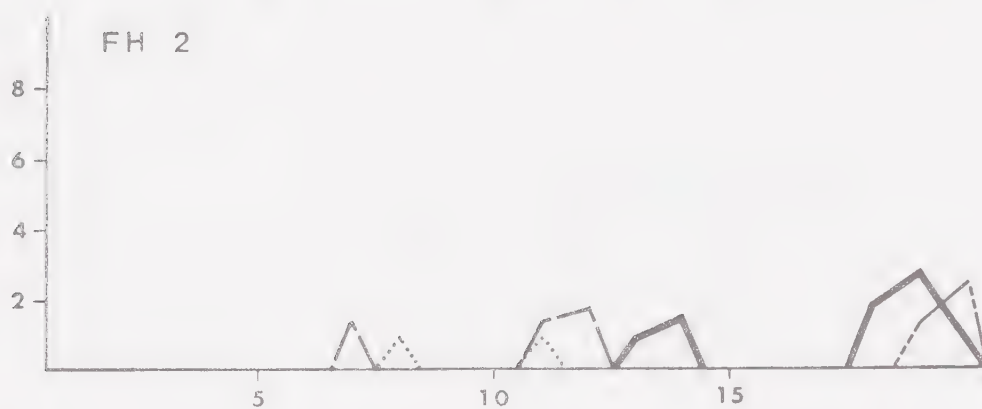
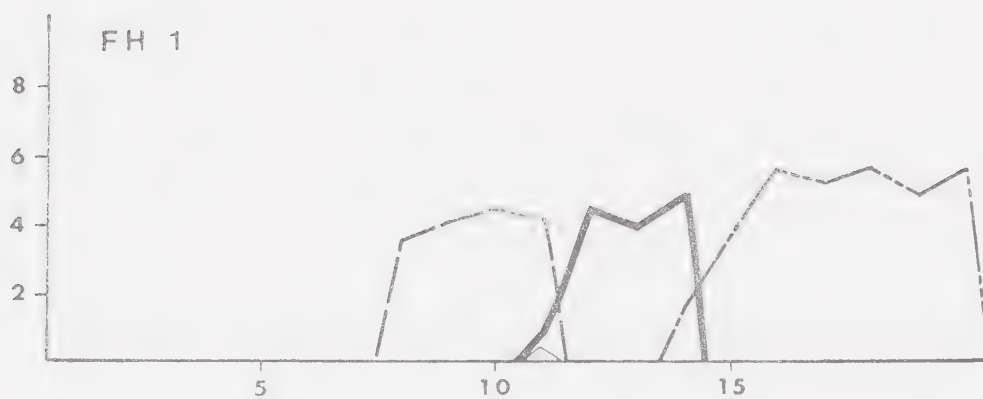


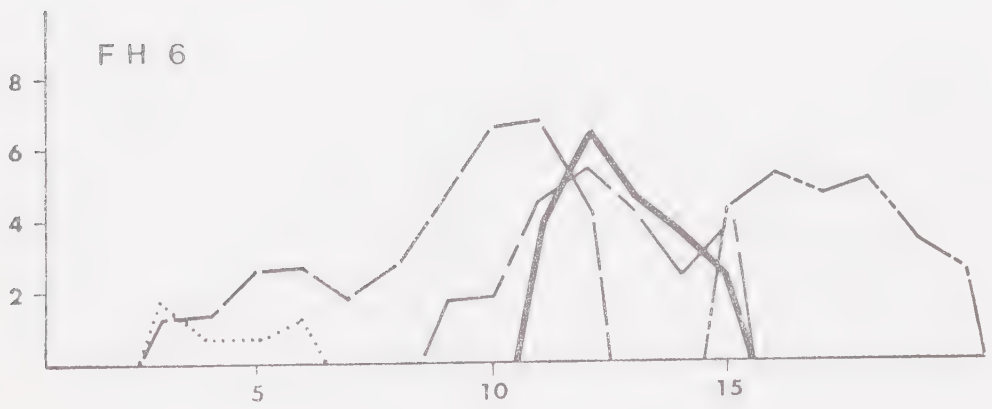
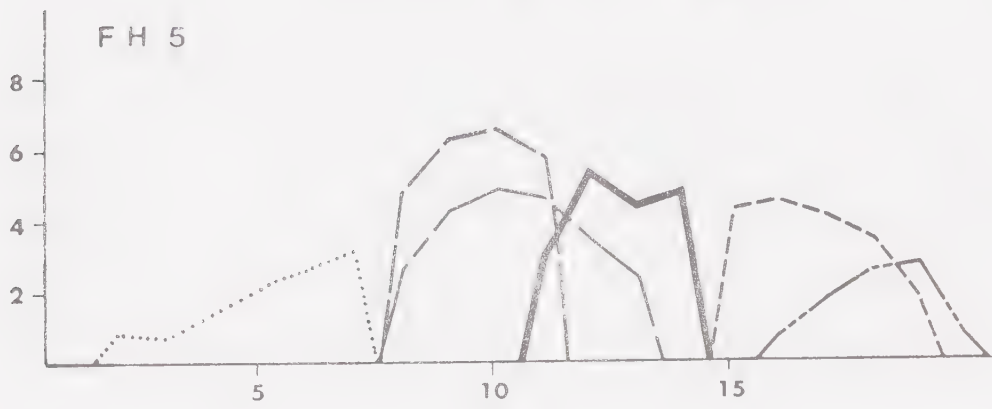
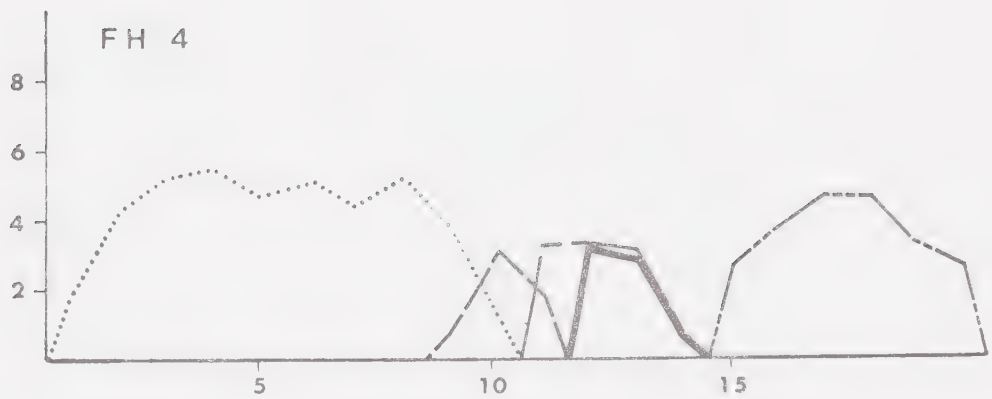


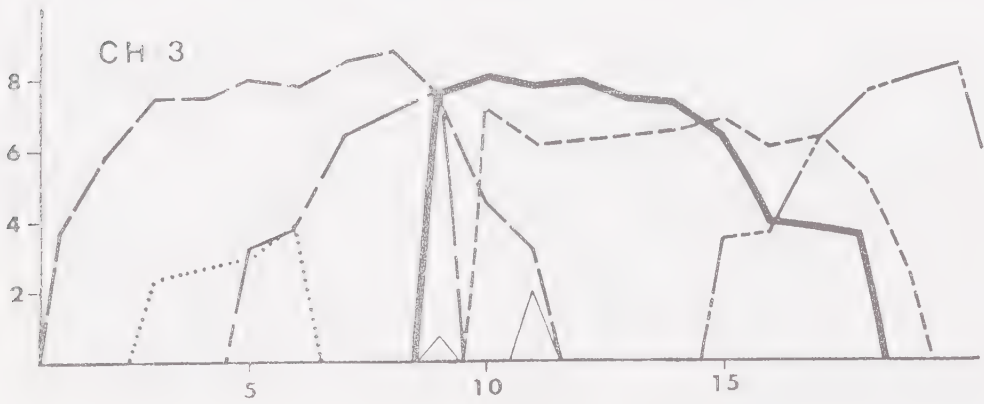
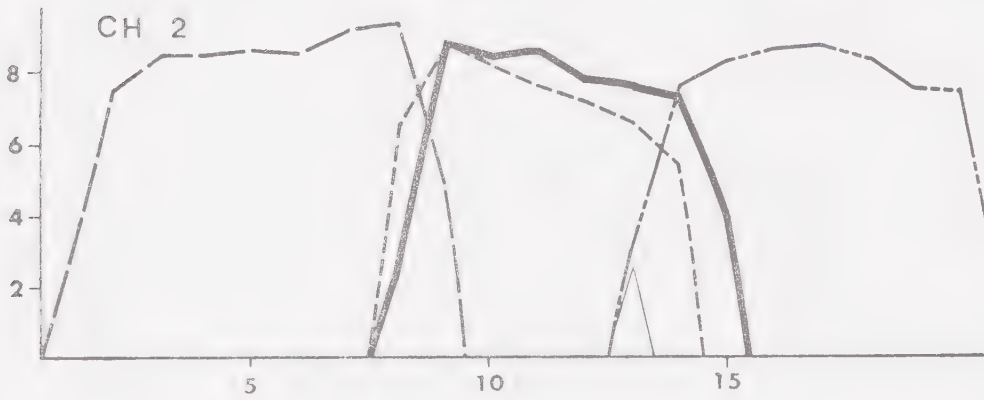
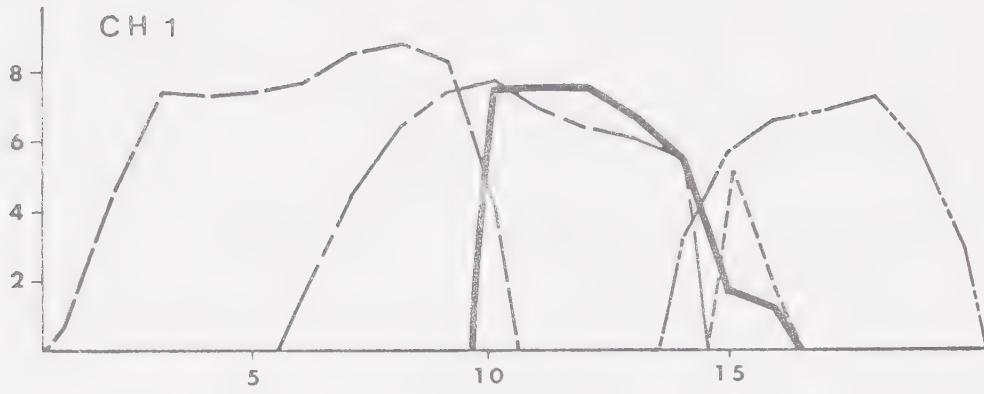


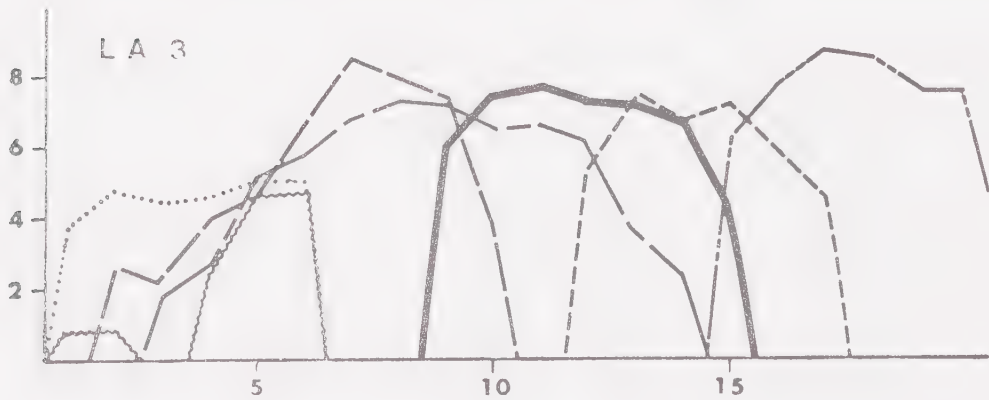
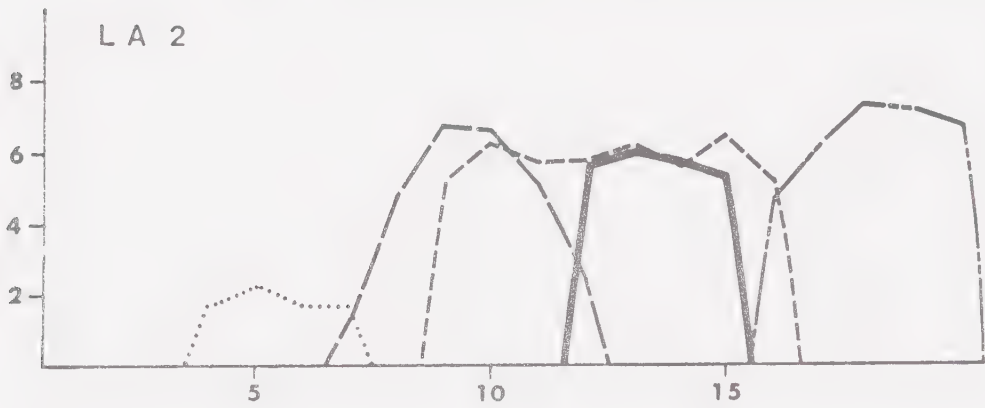
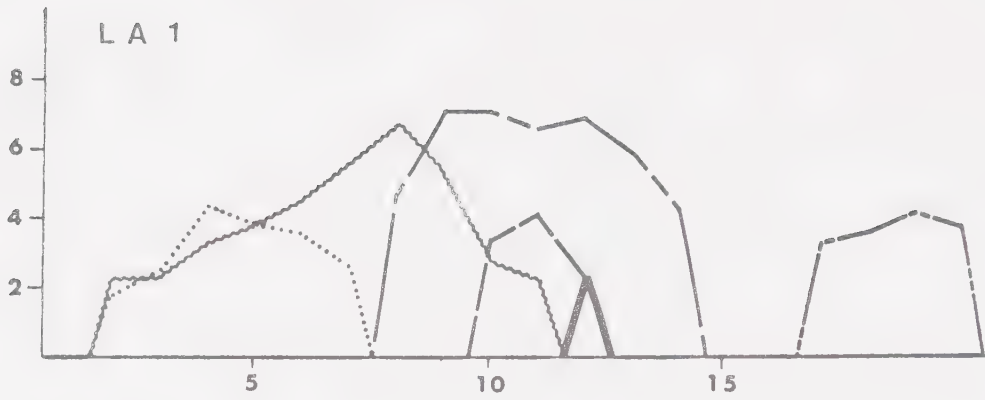


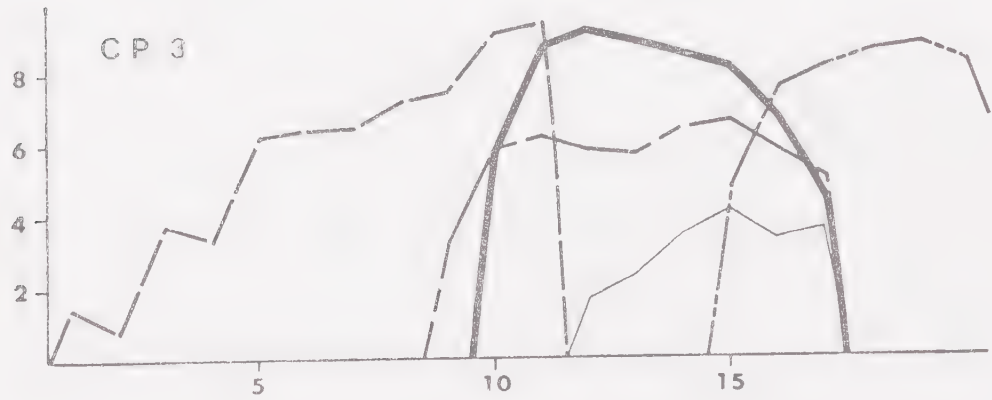
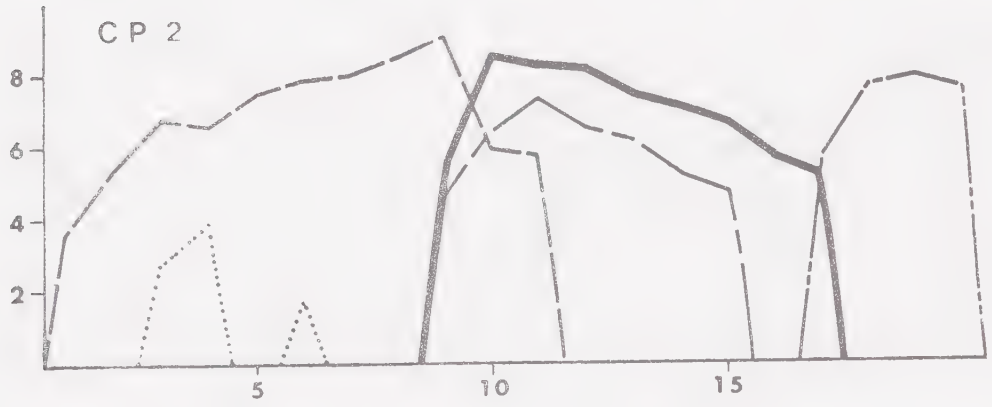
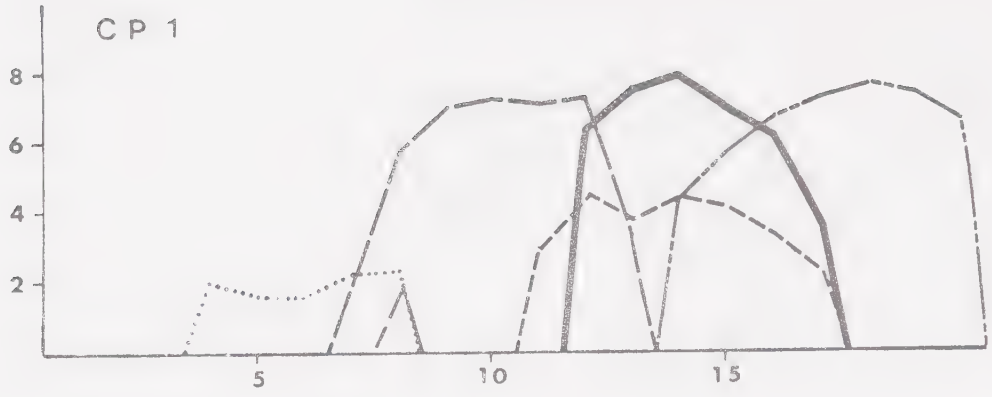


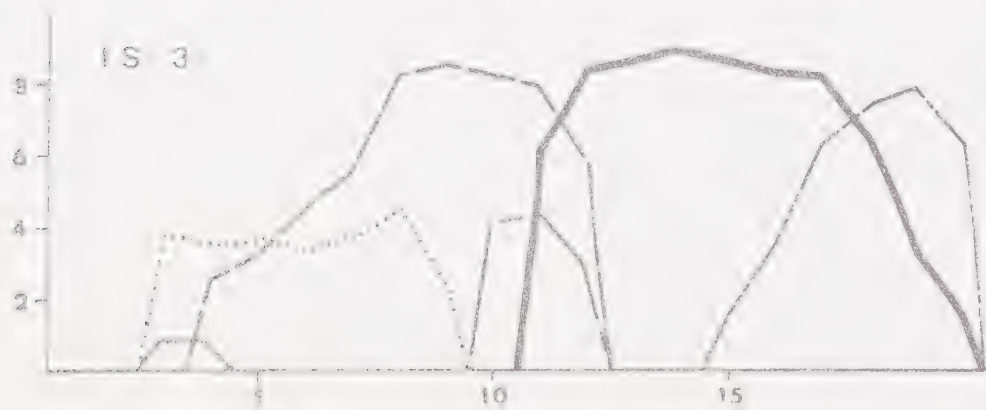
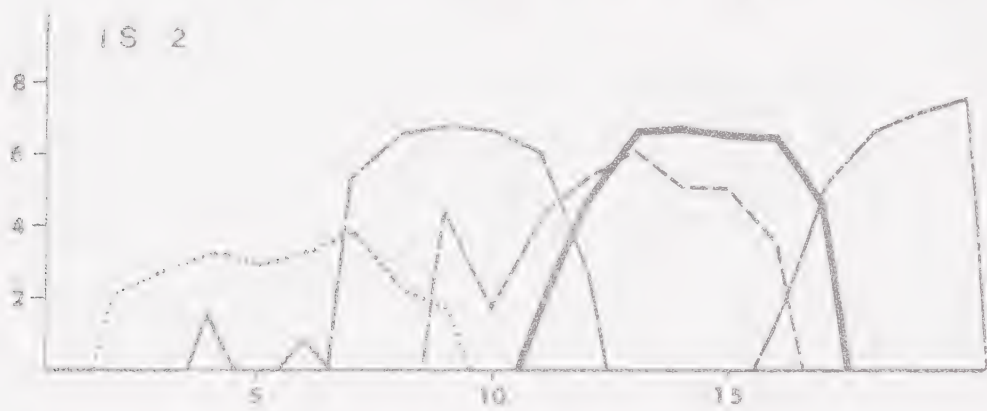
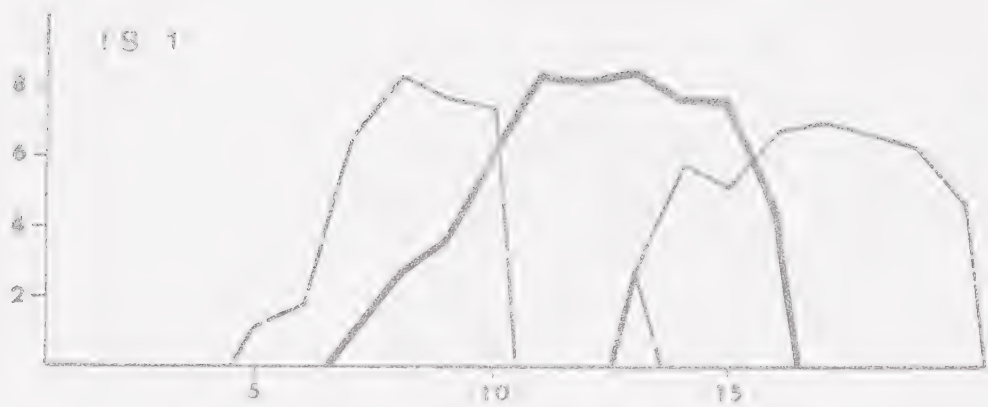


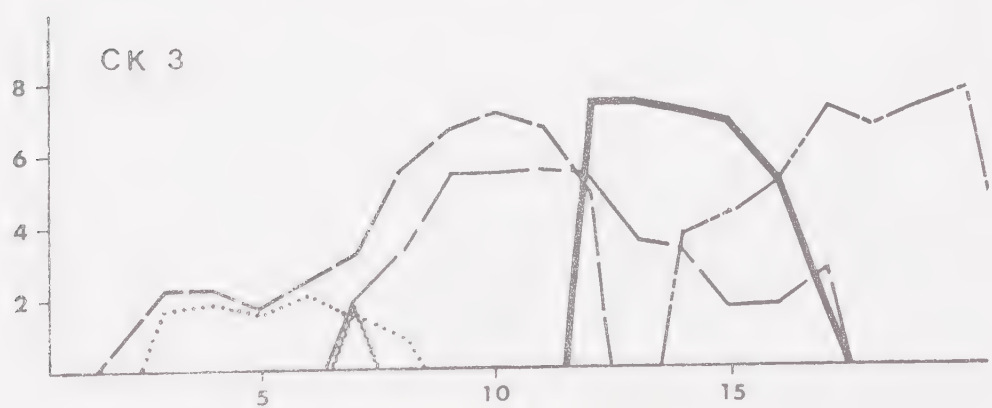
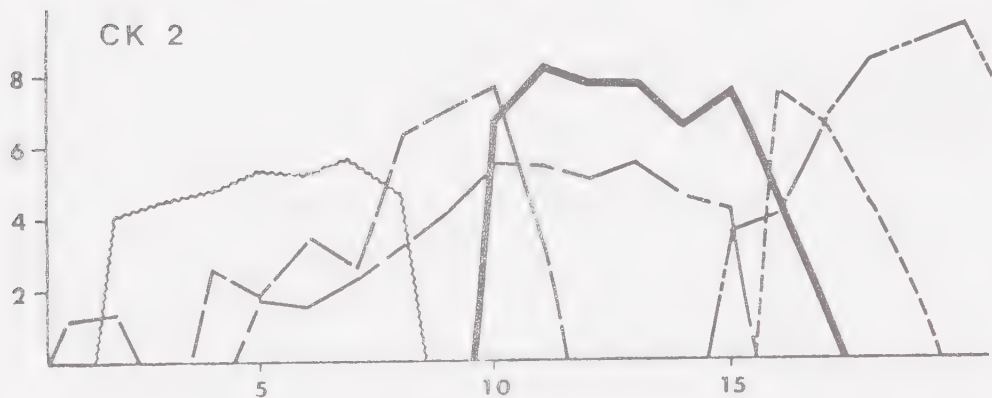
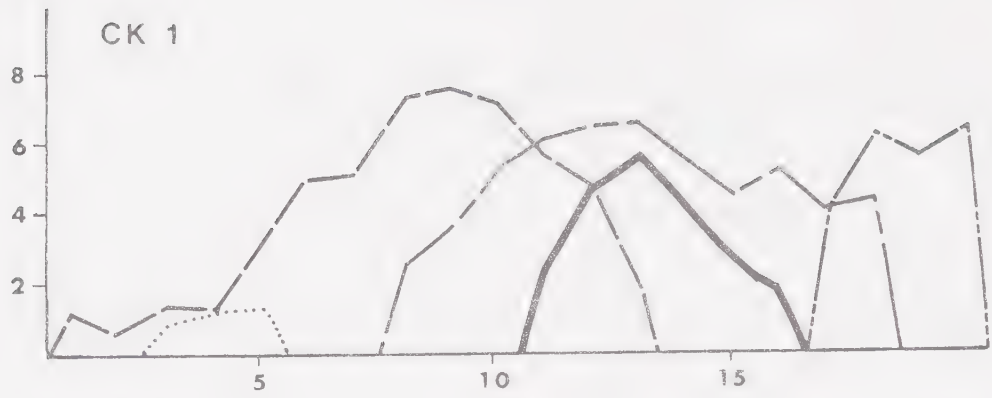


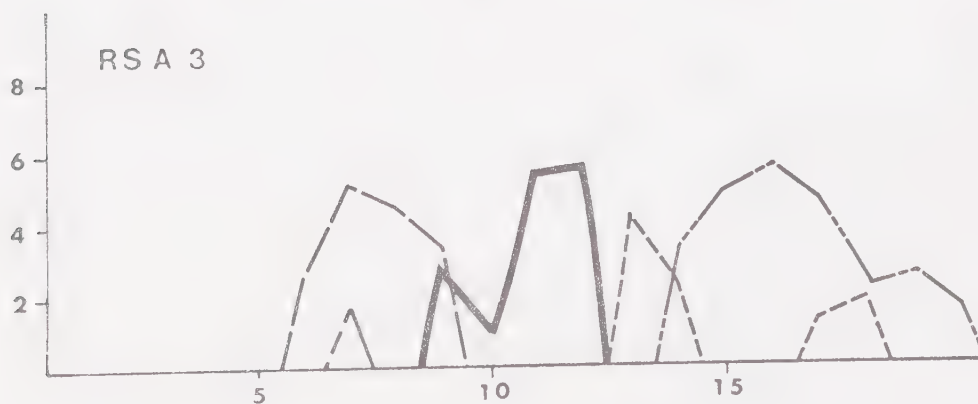
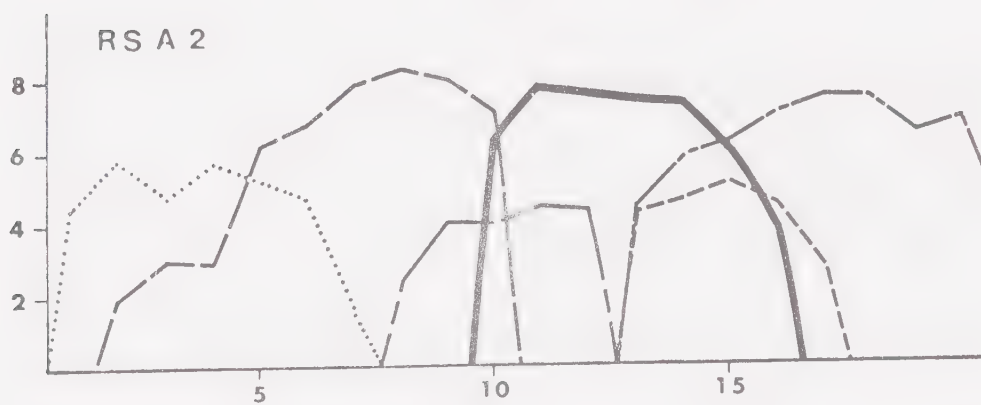
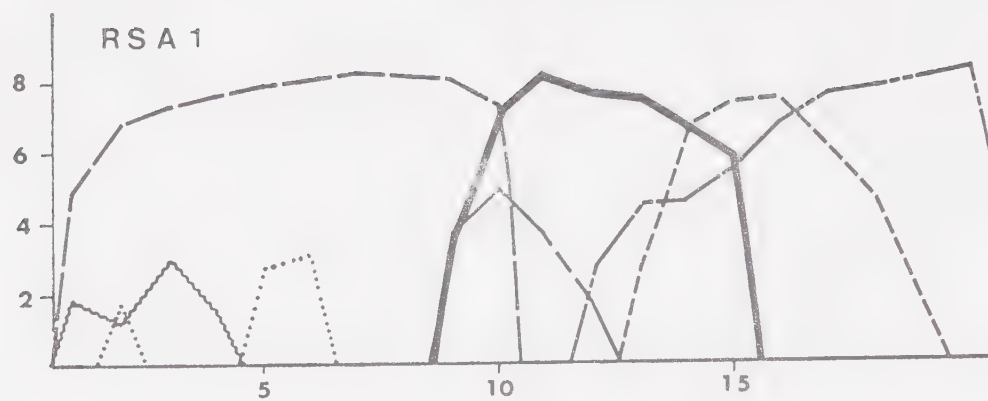


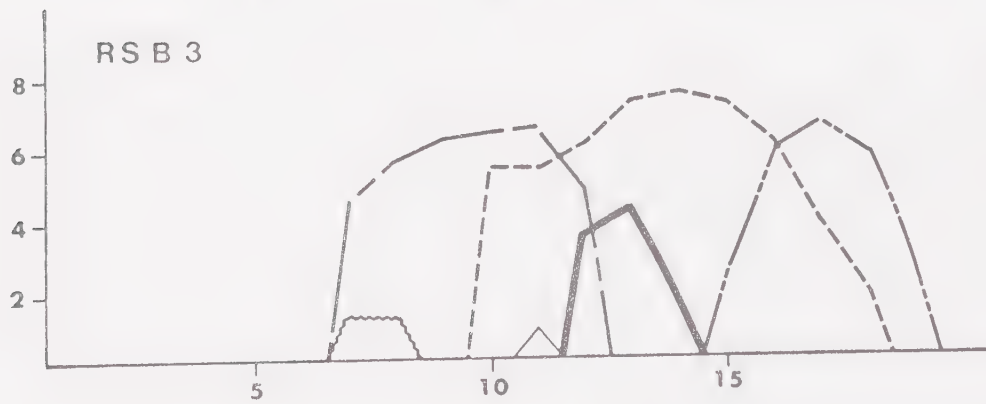
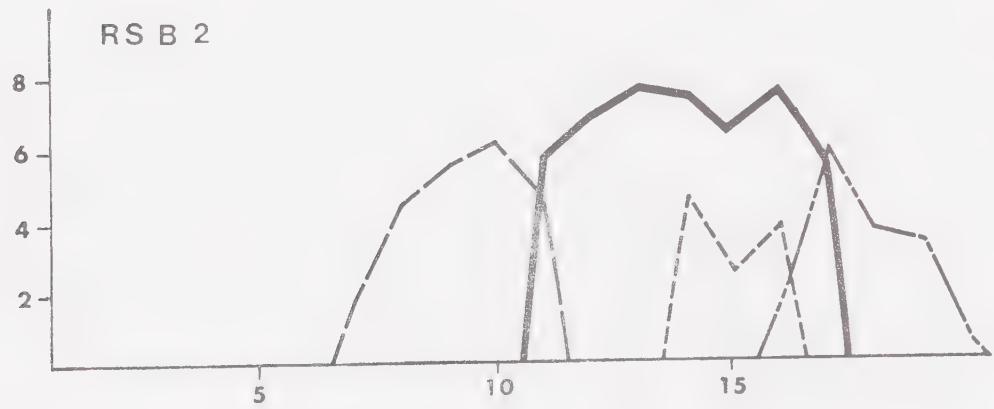
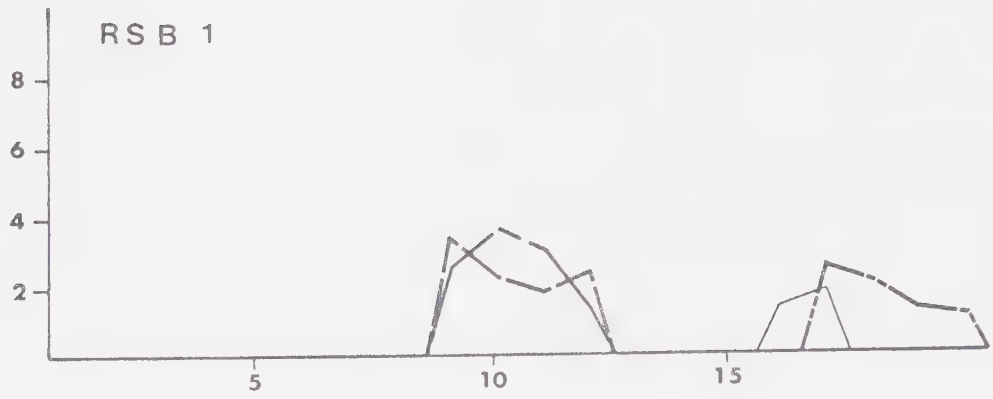


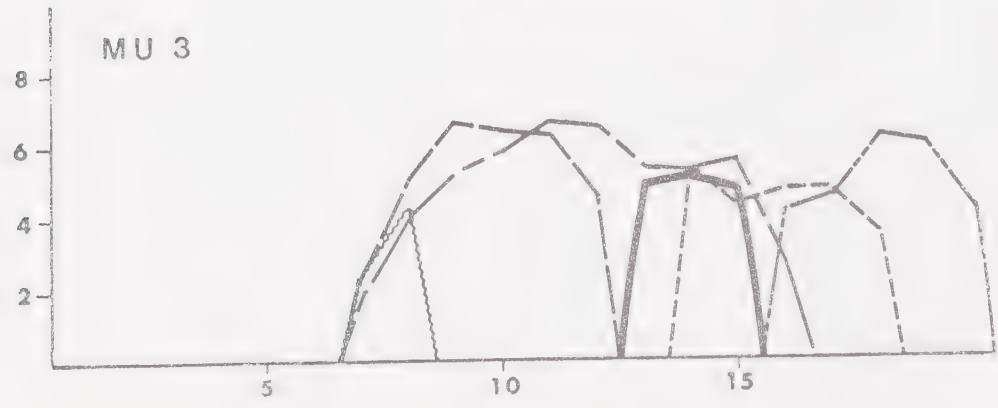
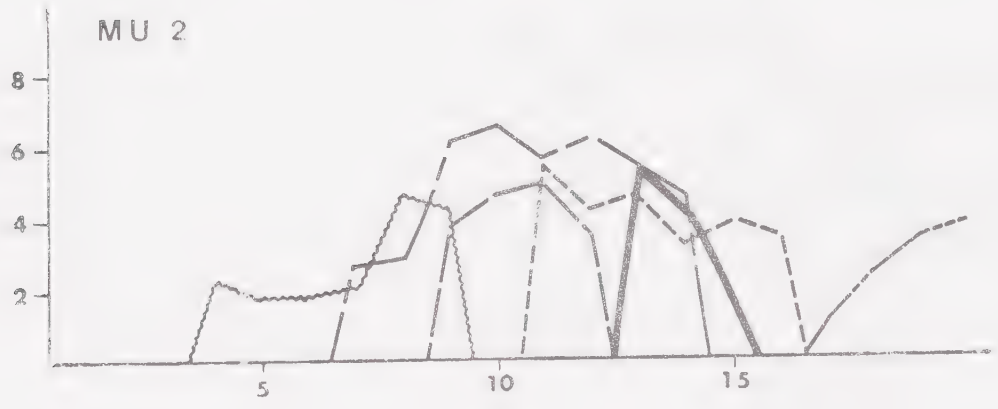
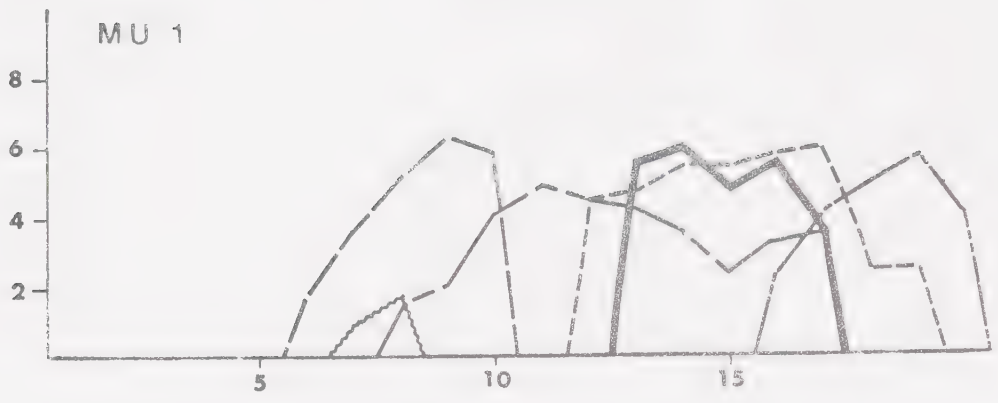


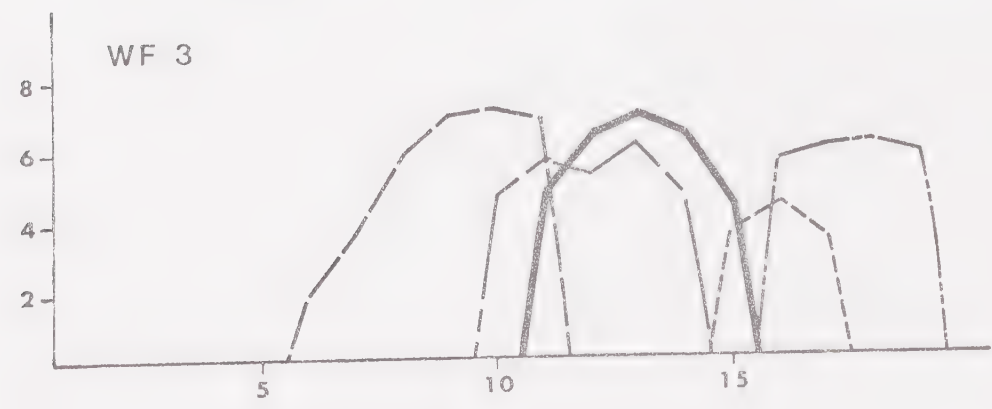
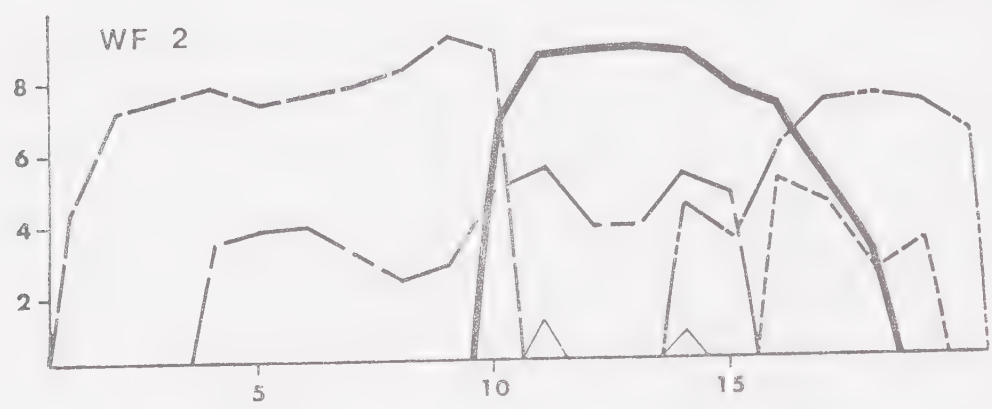
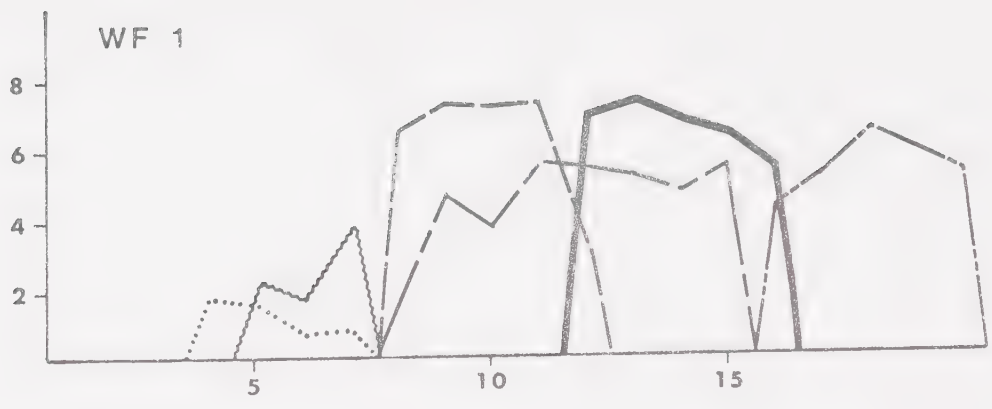












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